

Article

Effects of Biological Soil Crust Development on Extractable Nutrient Fractions in Adjacent Surface Soils of the Gurbantunggut Desert

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Abstract

Biological soil crusts (BSCs) are important components of dryland ecosystems, yet nutrient patterns in adjacent uncovered soils remain unclear. We surveyed 70 sites across the Gurbantunggut Desert and collected 209 composite samples from the adjacent 0–5 cm surface-soil layer, categorized into three groups: uncrusted bare sand ($n = 32$), soil adjacent to algal–lichen crusts ($n = 48$), and soil adjacent to moss crusts ($n = 129$), with bare sand serving as the uncrusted reference category. The results showed that: (1) total nitrogen differed among the three BSC-associated soil categories ($p = 0.041$), whereas soil organic carbon, total phosphorus, and total potassium did not (all $p > 0.05$); (2) NO_3^- -N, NH_4^+ -N, extractable inorganic N, NaHCO_3 -extractable phosphorus, and NH_4OAc -extractable potassium differed significantly among categories (all $p < 0.001$) and were generally highest in soil adjacent to moss crusts; and (3) random forest models explained approximately 38–65% of nutrient variation and identified EC, total nitrogen, and the site-level BSC metric as the leading predictors. The final piecewise structural equation model explained 35.3–76% of nutrient variation. These findings indicate marked regional heterogeneity in extractable nutrient fractions associated with different BSC types.

Keywords: algal–lichen crust; moss crust; dryland; nitrogen; phosphorus; potassium



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1. Introduction

Dryland soils support diverse microbial communities and regulate important biogeochemical processes, particularly carbon and nitrogen cycling [1,2]. Desert nutrient dynamics are constrained by limited precipitation and sparse vegetation and are further shaped by plant nutrient-acquisition strategies, litter decomposition, and spatial variation in plant–soil stoichiometry [3–6]. Under these conditions, biological soil crusts (BSCs), formed by cyanobacteria, algae, lichens, mosses, fungi, and other microorganisms, constitute an important component of the soil surface [7,8].

BSCs are surface communities formed through close associations between soil particles and phototrophic and heterotrophic organisms [8,9]. These communities are also sensitive to global environmental change, and their degradation may intensify land degradation

in drylands [10,11]. They stabilize the soil surface and reduce erosion [9,12], regulate soil water balance [13], and influence soil fertility and microbial communities [14–16]. BSCs can also affect the growth and physiological performance of vascular plants [17]. Based on their dominant phototrophic organisms, BSCs are commonly classified as algal-, lichen-, and moss-dominated crusts [8]. These crust types are associated with differences in community composition, surface properties, patch structure, and ecological functioning [15,18–24]. However, spatial differences among crust types do not demonstrate a temporal successional sequence. Therefore, this study treats algal–lichen and moss crusts as distinct BSC types and bare sand as an uncrusted reference.

BSCs are closely associated with nutrient cycling in drylands. Carbon fixation and nitrogen transformation by crust-forming organisms can influence soil carbon and nitrogen pools [16,25–27]. BSCs may also intercept nutrient-bearing dust [28], contribute to phosphorus transformation [29,30], influence potassium accumulation [31,32], and release nutrients during the decomposition of crust-forming organisms [33,34]. Most previous studies have examined the crust layer or the soil directly beneath it [24,35–39]. Although several studies have investigated edge effects or horizontal nutrient gradients around moss-crust patches [40,41], regional nutrient patterns in uncovered soils adjacent to different BSC types remain poorly understood.

BSCs are spatially heterogeneous across the Gurbantunggut Desert and vary with climatic, geographic, and edaphic conditions [23,42–44]. We therefore compared three categories of 0–5 cm surface soil: uncrusted bare sand, soil adjacent to algal–lichen crusts, and soil adjacent to moss crusts. Specifically, we examined: (1) whether soil organic carbon and total nitrogen, phosphorus, and potassium differed among categories; (2) whether extractable inorganic N, NaHCO_3 -extractable phosphorus, and NH_4OAc -extractable potassium differed among categories; and (3) how these nutrient patterns were associated with geographic location, climate, BSC category, soil pH, and electrical conductivity.

2. Materials and Methods

2.1. Study Area

The study was conducted in the Gurbantunggut Desert, located in the Junggar Basin of northern Xinjiang, China ($44^\circ 11'–46^\circ 20' \text{ N}$, $84^\circ 31'–90^\circ 00' \text{ E}$). The desert covers approximately $4.88 \times 10^4 \text{ km}^2$, of which fixed and semi-fixed dunes account for approximately 87% [42,43]. It has a temperate continental climate, with annual precipitation of 70–260 mm and potential evaporation of approximately 2606.6 mm. Summer temperatures can exceed 40°C , whereas winter temperatures can fall below -20°C [35,38,45]. Vegetation is sparse, and BSCs occur as spatially heterogeneous patches across the desert [42–44].

2.2. Sampling Design and Sample Collection

Seventy sampling sites were established at approximately 10-km intervals along the desert highway (Figure 1). To reduce anthropogenic disturbance, each site was located approximately 10 km from the highway. All sampling was conducted at the bases of dunes to maintain comparable topographic conditions among sites.

At each site, three spatially separated $10 \text{ m} \times 10 \text{ m}$ quadrats were established, with a minimum distance of 10 m between quadrats. BSC types were identified according to dominant visible organisms and surface morphology, following established definitions and regional studies [8,22–24,42,43]. Bare sand was defined as loose, unconsolidated sand without continuous biocrust cover; algal–lichen crusts were characterized by cohesive surfaces dominated by cyanobacterial or algal films and/or visible lichen thalli; and moss crusts were identified by dominant visible moss shoots.

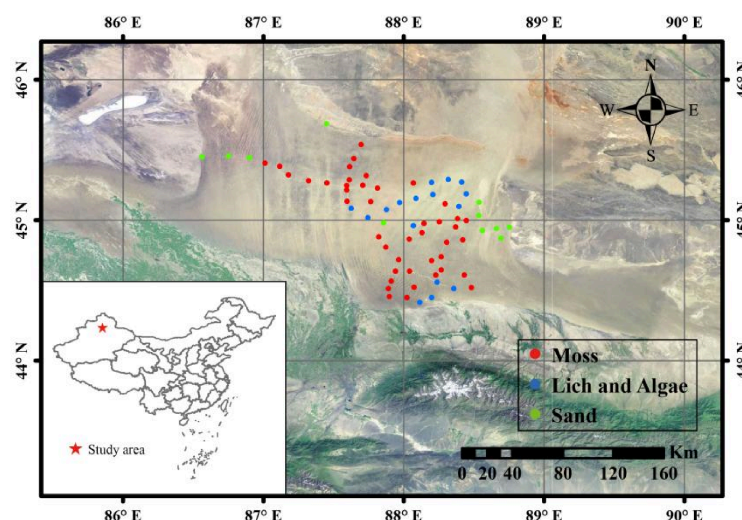


Figure 1. Locations of the 70 sampling sites across the Gurbantunggut Desert, northwestern China.

BSC cover and crust thickness were recorded in each quadrat using a 1 m × 1 m grid-based survey [22]. A site-level BSC metric was calculated by integrating BSC developmental category and fractional cover. Bare sand, algal–lichen crust, and moss crust were assigned values of 0, 1, and 2, respectively, according to the regional BSC developmental classification [43]. The quadrat-level BSC score was calculated as:

$$\text{BSC score} = \sum (\text{BSC category value} \times \text{fractional cover}).$$

For example, a quadrat with 50% algal–lichen crust and 30% moss crust had a score of $(1 \times 0.50) + (2 \times 0.30) = 1.10$. The three quadrat-level scores were averaged to obtain the site-level BSC metric. This unitless metric ranged from 0 to 2, with higher values indicating greater overall BSC development at the site level. Crust thickness was recorded separately and was not included in the metric.

Soil samples were collected more than 50 cm from shrubs to minimize shrub-associated fertile-island effects [46]. Within each quadrat, five subsamples were collected from the adjacent uncovered 0–5 cm surface-soil layer using a five-point sampling method and homogenized to form one quadrat-level composite sample. Thus, five subsamples were nested within each quadrat, and three quadrats were nested within each sampling site.

A total of 210 quadrat-level composite samples were planned, of which 209 were available for analysis: uncrusted bare sand ($n = 32$), soil adjacent to algal–lichen crusts ($n = 48$), and soil adjacent to moss crusts ($n = 129$). The unequal sample sizes reflected the actual spatial occurrence of the three categories in the field. Samples were sealed, transported to the laboratory on dry ice, homogenized, and divided into subsamples for chemical analyses.

2.3. Soil Analyses and Climate Data

Soil organic carbon (SOC), total nitrogen (TN), total phosphorus (TP), total potassium (TK), nitrate nitrogen (NO_3^- -N), ammonium nitrogen (NH_4^+ -N), NaHCO_3 -extractable phosphorus (AP), NH_4OAc -extractable potassium (AK), pH, and electrical conductivity (EC) were measured.

TN was determined using the Kjeldahl method following digestion with concentrated H_2SO_4 and quantified using an automatic Kjeldahl analyzer (Kjeltec 8400, FOSS Analytical A/S, Hillerød, Denmark). TP was measured using the molybdenum–antimony colorimetric method with a UV-visible spectrophotometer (UV-2600i, Shimadzu Corporation, Kyoto, Japan), whereas TK was determined using inductively coupled plasma optical emission

spectrometry (Optima 3000-DV ICP, PerkinElmer Inc., Shelton, CT, USA). NO_3^- -N and NH_4^+ -N were extracted with KCl and determined colorimetrically using a continuous-flow autoanalyzer (Auto-Analyzer 3, SEAL AA3, Bran+Luebbe, Norderstedt, Germany). Extractable inorganic nitrogen (EIN) was operationally defined as the sum of KCl-extractable NO_3^- -N and NH_4^+ -N.

SOC was measured by combustion using a total organic carbon analyzer (multi N/C 3100, Analytik Jena GmbH, Jena, Germany) after the removal of inorganic carbon with 1 mol L⁻¹ HCl. AP was extracted with NaHCO_3 and determined colorimetrically using the UV-visible spectrophotometer described above, whereas AK was extracted with 1 mol L⁻¹ NH_4OAc , filtered, and determined using an atomic absorption spectrophotometer (Model 2380, PerkinElmer Inc., Waltham, MA, USA). Soil pH and EC were measured in soil-to-water suspensions at ratios of 1:2.5 and 1:5 using a SevenCompact S220 pH meter and a SevenCompact S230 conductivity meter, respectively (Mettler-Toledo GmbH, Greifensee, Switzerland). All chemicals and reagents used in the analyses were of analytical grade and were purchased from Sinopharm Chemical Reagent Co., Ltd. (Shanghai, China).

Mean annual temperature (MAT, °C) and mean annual precipitation (MAP, mm) for each sampling site were obtained from the China Meteorological Data Service Center (<http://data.cma.cn/site/index.html>, accessed on 12 June 2026) and the Resource and Environment Science and Data Center of the Chinese Academy of Sciences (<http://www.resdc.cn>, accessed on 12 June 2026). Climate data were matched to the geographic coordinates of each sampling site and averaged over the period 1995–2015.

2.4. Statistical Analyses

All statistical analyses were conducted in R version 4.1.2 (R Foundation for Statistical Computing, Vienna, Austria). Because quadrats were nested within sampling sites, site-level clustering was accounted for in all analyses.

Differences among the three surface-soil categories were tested using linear mixed-effects models fitted with the lme4 package (version 1.1-27.1), with surface-soil category as a fixed effect and site as a random intercept. Model convergence was checked using the performance package (version 0.8.0). Significant overall effects were followed by Tukey-adjusted pairwise comparisons of estimated marginal means using the emmeans package (version 1.7.0). Statistical significance was set at $p < 0.05$.

For Pearson correlation, random forest, and piecewise structural equation modelling, quadrat-level measurements were averaged within sites, yielding 70 site-level observations.

Pearson correlations were calculated among site-level SOC, total nutrient variables, extractable nutrient fractions, pH, EC, MAT, MAP, longitude, latitude, and the site-level BSC metric. Complete correlation coefficients, p values, and sample sizes are provided in Table S2.

Random forest models for NO_3^- -N, NH_4^+ -N, NaHCO_3 -extractable P, and NH_4OAc -extractable K were fitted using the rfPermute package (version 2.5) based on the random forest algorithm [47]. Each model used 500 trees and 1000 permutation replicates, with mtry values of four for the N models and three for the P and K models. Predictor importance was assessed using permutation-based out-of-bag error, and model performance was evaluated using mean squared error, root mean squared error, and explained variance. Partial-dependence plots were generated using the pdp package (version 0.7.0).

Piecewise structural equation modelling was conducted using the piecewiseSEM package (version 2.1.2) [48–50]. Paths were removed only when they had an absolute standardized coefficient below 0.05, were nonsignificant ($p > 0.05$), and lacked clear ecological support. Nonsignificant paths representing core a priori hypotheses were retained when their removal did not improve model fit and are shown as dashed arrows in Figure 6. Model

fit was evaluated using Fisher's C, the chi-square test, Akaike's information criterion, and tests of directed separation.

3. Results

3.1. Differences in Soil Chemical Properties Among BSC-Associated Soil Categories

Total nitrogen differed significantly among the three BSC-associated soil categories ($F_{2,206} = 3.25$, $p = 0.041$). TN was higher in soil adjacent to moss crusts than in algal–lichen–crust-associated soil, whereas bare sand did not differ significantly from either category. In contrast, SOC, TP, and TK did not differ significantly among categories (all $p > 0.05$; Table 1).

Table 1. Soil organic carbon and total nutrient concentrations in the three BSC-associated surface-soil categories.

BSC-Associated Soil Category	n	TN (mg/g)		TP (mg/g)		TK (mg/g)		SOC (mg/g)	
		Mean $\pm$ SE	CV	Mean $\pm$ SE	CV	Mean $\pm$ SE	CV	Mean $\pm$ SE	CV
Sand	32	0.26 $\pm$ 0.01	0.25	0.42 $\pm$ 0.01	0.15	20.16 $\pm$ 0.39	0.11	1.95 $\pm$ 0.11	0.33
Lichen and Algae	48	0.25 $\pm$ 0.01	0.29	0.41 $\pm$ 0.01	0.13	20.39 $\pm$ 0.30	0.1	1.97 $\pm$ 0.08	0.29
Moss	129	0.28 $\pm$ 0.01	0.31	0.42 $\pm$ 0.01	0.13	20.00 $\pm$ 0.17	0.1	1.95 $\pm$ 0.06	0.35

Note: Values are presented as means $\pm$ standard errors (SE). CV represents the coefficient of variation, and n represents the number of quadrat-level composite errors. Differences among the three surface-soil categories were evaluated using linear mixed-effects models, with surface-soil category as a fixed effect and sampling site as a random intercept. When the overall category effect was significant, pairwise comparisons of estimated marginal means were conducted using Tukey adjustment.

All measured extractable nutrient fractions differed significantly among categories (all $p < 0.001$; Figure 2). NO_3^- -N, NH_4^+ -N, extractable inorganic N, and NaHCO_3 -extractable P were highest in soil adjacent to moss crusts, intermediate in algal–lichen–crust-associated soil, and lowest in bare sand. The corresponding mean values for soil adjacent to moss crusts, algal–lichen–crust-associated soil, and bare sand were 10.79, 7.98, and 3.82 mg kg^{-1} for NO_3^- -N; 14.87, 11.19, and 8.36 mg kg^{-1} for NH_4^+ -N; 25.66, 19.16, and 12.18 mg kg^{-1} for extractable inorganic N; and 4.24, 3.63, and 2.33 mg kg^{-1} for NaHCO_3 -extractable P. NH_4OAc -extractable K was lower in bare sand than in both BSC-associated soil categories, whereas soils adjacent to algal–lichen and moss crusts did not differ significantly from each other.

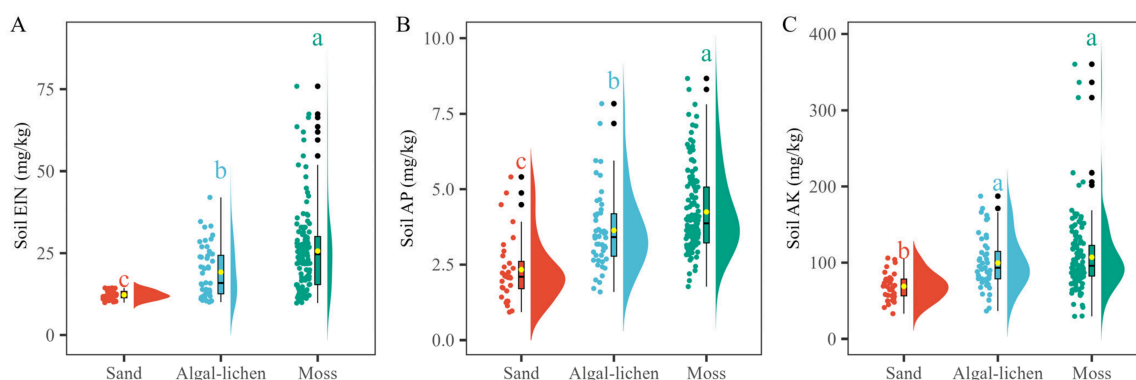


Figure 2. Extractable nutrient concentrations in the three BSC-associated soil categories. Panels show (A) extractable inorganic nitrogen (EIN), (B) NaHCO_3 -extractable phosphorus (AP), and (C) NH_4OAc -extractable potassium (AK). Different lowercase letters indicate significant differences among categories ($p < 0.05$). Red, blue, and green represent sand, algal–lichen, and moss categories, respectively. Colored points represent individual quadrat-level composite samples, half-violin plots show the data distributions, boxplots show the medians and interquartile ranges, yellow dots indicate the means, and black dots indicate outliers.

Soil pH also differed significantly among categories ($F_{2,206} = 5.28$, $p = 0.006$). It was lower in algal–lichen–crust-associated soil than in bare sand and soil adjacent to moss crusts, whereas the latter two categories did not differ significantly. EC was higher in soil adjacent to moss crusts than in bare sand and algal–lichen–crust-associated soil ($F_{2,206} = 15.37$, $p < 0.001$), with no significant difference between the latter two categories (Figure 3).

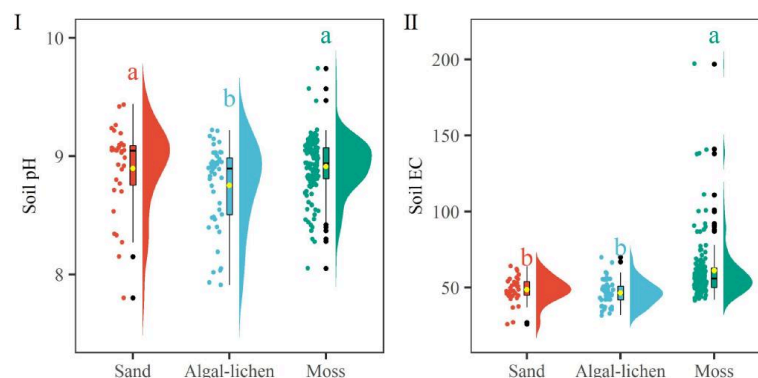


Figure 3. Soil pH and electrical conductivity (EC) in the three BSC-associated soil categories. Panels show (I) soil pH and (II) soil EC. Different lowercase letters indicate significant differences among categories ($p < 0.05$). Red, blue, and green represent sand, algal–lichen, and moss categories, respectively. Colored points represent individual quadrat-level composite samples, half-violin plots show the data distributions, boxplots show the medians and interquartile ranges, yellow dots indicate the means, and black dots indicate outliers.

3.2. Relationships Among Soil Nutrient Variables

Pearson correlation analysis was used to examine relationships among total and extractable nutrients, climatic variables, soil chemical properties, geographic factors, and the site-level BSC metric (Figure 4). The complete Pearson correlation matrix is provided in Table S2. SOC was significantly positively correlated with TN and TP in all three BSC-associated soil categories. SOC was also significantly positively correlated with TK in soils adjacent to algal–lichen and moss crusts, whereas the SOC–TK relationship was not significant in bare sand (Figure 5). Among the total nutrient variables, TN was positively correlated with TP and TK, whereas TP was negatively correlated with TK.

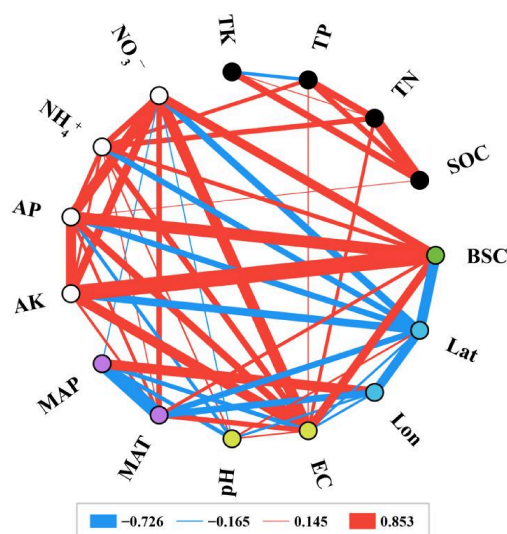


Figure 4. Pearson correlation network among soil nutrients, environmental variables, geographic factors, and the site-level BSC metric. Red and blue lines indicate positive and negative correlations, respectively, and line width represents correlation strength.

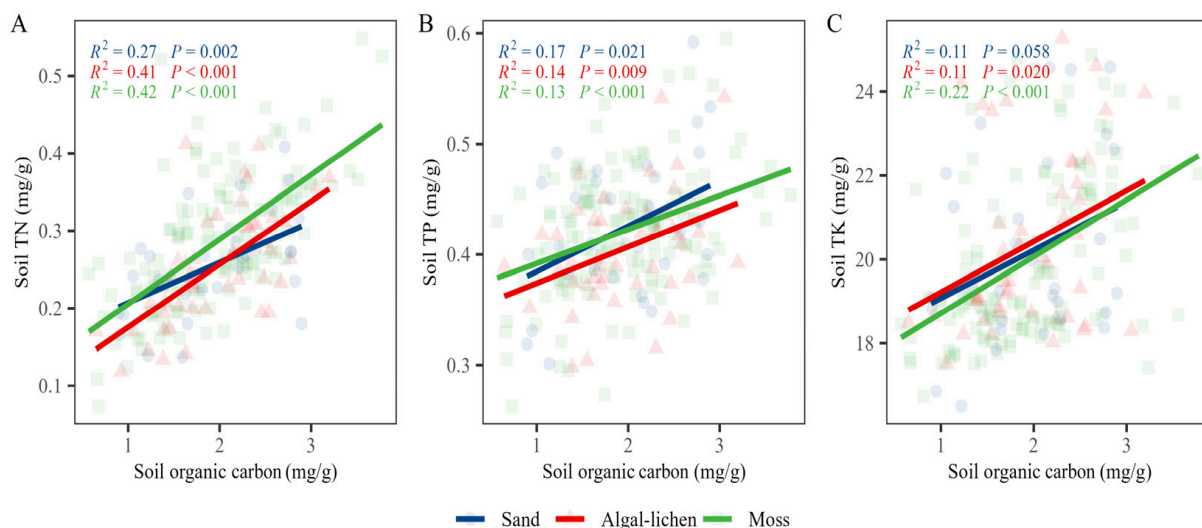


Figure 5. Relationships between soil organic carbon and total nitrogen (A), total phosphorus (B), and total potassium (C) in the three BSC-associated soil categories. Blue circles, red triangles, and green squares represent sand, algal-lichen, and moss categories, respectively. Points represent individual quadrat-level composite samples, and solid lines represent the fitted linear regressions for the corresponding categories.

The site-level BSC metric was positively correlated with all measured extractable nutrient variables but was not significantly correlated with SOC or total nutrients. Latitude was negatively correlated with both the site-level BSC metric and extractable nutrients. $\text{NH}_4^+\text{-N}$ was positively correlated with TN and TP, whereas most other correlations between total and extractable nutrients were not significant.

3.3. Major Predictors Identified by Random Forest Analysis

The random forest models explained approximately 38–65% of the variation in the four extractable nutrient variables (Figure S1; Table S1). EC was the leading predictor of $\text{NO}_3^-\text{-N}$, TN was the leading predictor of $\text{NH}_4^+\text{-N}$, and the site-level BSC metric was the leading predictor of extractable P and K (all permutation-based $p < 0.001$; Figure S1). Partial-dependence plots showed generally positive, nonlinear modelled associations between the leading predictors and the corresponding nutrient variables (Figure S2). Detailed model results are provided in Table S1.

3.4. Structural Associations Among Environmental and Nutrient Variables

The SEM explained 60%, 35%, 54%, and 76% of the variance in $\text{NO}_3^-\text{-N}$, $\text{NH}_4^+\text{-N}$, $\text{NaHCO}_3\text{-extractable P}$, and $\text{NH}_4\text{OAc-extractable K}$, respectively (Figure 6). Longitude, latitude, MAP, and MAT were negatively associated with the site-level BSC metric. The site-level BSC metric was negatively associated with pH but positively associated with EC, extractable P, and extractable K. Soil pH was negatively associated with $\text{NO}_3^-\text{-N}$ and extractable P but positively associated with $\text{NH}_4^+\text{-N}$. EC was positively associated with all four extractable nutrient variables. Extractable P was positively associated with $\text{NO}_3^-\text{-N}$ and $\text{NH}_4^+\text{-N}$, whereas extractable K was negatively associated with $\text{NH}_4^+\text{-N}$. The model showed satisfactory fit ($\chi^2 = 16.17$, $\text{df} = 15$, $p = 0.371$; Fisher's C = 15.56, $\text{df} = 28$, $p = 0.972$).

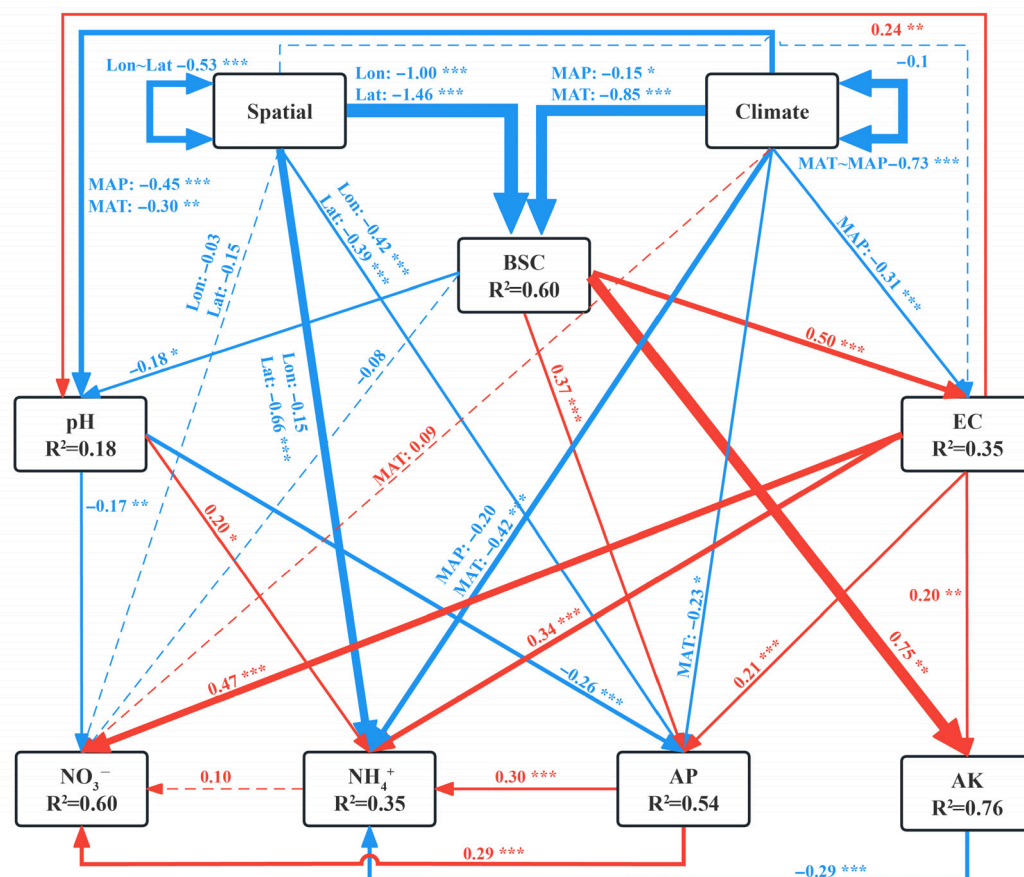


Figure 6. Final piecewise structural equation model showing statistical associations among spatial, climatic, site-level BSC, soil chemical, and extractable nutrient variables. Numbers beside the paths are standardized path coefficients, and path width represents association strength. Red and blue paths indicate positive and negative associations, respectively. Solid paths indicate statistically significant associations ($p < 0.05$), whereas dashed paths indicate nonsignificant associations retained because they represented core a priori relationships and their removal did not improve model fit. R^2 values are shown for endogenous variables. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$. Model fit: Fisher's $C = 15.558$, $df = 28$, $p = 0.972$.

4. Discussion

Among the total nutrient variables, only TN differed significantly among the three BSC-associated soil categories, whereas SOC, TP, and TK showed no significant differences. TN was higher in soil adjacent to moss crusts than in algal-lichen-crust-associated soil, while bare sand did not differ significantly from either category. Previous studies have mainly focused on nutrient changes within BSC layers or in soils directly beneath them [24,36–39,51,52]. Nutrient accumulation around moss crusts may be related to rhizoids and associated microorganisms in the shallow substrate [35,38]. At the regional scale, however, total nutrient patterns in adjacent uncovered soils may also be strongly influenced by spatial heterogeneity, plant inputs, and mineral weathering [53–56].

In contrast, extractable nutrient fractions showed clearer differences among the BSC-associated soil categories. NO_3^- -N, NH_4^+ -N, extractable inorganic N, and NaHCO_3 -extractable P were highest in soil adjacent to moss crusts, intermediate in algal-lichen-crust-associated soil, and lowest in bare sand. NH_4OAc -extractable K was also higher in both BSC-associated categories than in bare sand. These patterns may reflect improved near-surface moisture conditions [13,57,58], microbial activity [16,39,52,59], soil stabilization [12,16,59,60], and nutrient-rich dust retention around BSC patches [28]. How-

ever, these processes were not directly measured and should be considered plausible explanations rather than demonstrated mechanisms.

Figures 4 and 5 showed that SOC was positively correlated with TN and TP in all three soil categories, whereas SOC was positively correlated with TK only in soils adjacent to algal-lichen and moss crusts. Plant litter and litter crusts can modify surface microhabitats, whereas the decomposition of litter and biocrust-forming organisms can release organic matter and nutrients into surface soils [33,61–63]. These processes may contribute to coordinated variation between SOC and N and P. Thus, SOC was closely coupled with TN and TP, whereas the relationship between SOC and TK may be more strongly constrained by mineral composition and weathering processes.

The correlation network and SEM indicated that extractable nutrient fractions in soils adjacent to BSC patches were associated with BSC characteristics, geographic gradients, climatic variables, and soil chemical properties, addressing the third study objective. BSCs are more abundant and continuously distributed in the southern Gurbantunggut Desert, whereas their distribution becomes increasingly fragmented toward the north, west, and east [23,42,43]. Changes in temperature, precipitation, and surface conditions along the latitudinal gradient may jointly affect BSC cover and nutrient patterns [44]. However, the short-term responses of desert soil micro- and mesofauna to elevated temperature and increased summer precipitation frequency may be limited [64]. Therefore, the negative relationships of latitude with the site-level BSC metric and several extractable nutrient variables likely reflect the combined variation in regional environmental gradients, BSC distribution, and nutrient turnover rather than the direct effect of a single factor.

The SEM further showed that the site-level BSC metric was negatively associated with soil pH but positively associated with EC. Algal-lichen-crust-associated soil had lower pH, whereas soil adjacent to moss crusts had higher EC, possibly reflecting local heterogeneity around BSC patches. Redistribution of water and nutrients around fertile islands can alter soil pH and salinity [46]. In addition, EC and pH are important variables influencing extracellular-enzyme activity [39]. The lower pH observed in algal-lichen-crust-associated soil is consistent with previous reports of changes in soil chemical properties during BSC development [24,65]. Such changes may influence microbial activity and nutrient cycling [41,52].

This study was based on a regional observational survey; therefore, the observed correlations and SEM pathways do not demonstrate causality or temporal BSC succession. It is important to note that KCl-extractable inorganic N, NaHCO_3 -extractable P, and NH_4OAc -extractable K are operationally defined chemical fractions and do not directly represent nutrients bioavailable for plant uptake. Actual plant availability is further influenced by dynamic field processes, including soil moisture, microbial immobilization, root exudation, and extracellular-enzyme activity, none of which were directly measured in this study. We therefore use the term “extractable nutrient fractions,” rather than “available nutrients,” throughout the manuscript to avoid overinterpreting the operational extraction results. In addition, soil bulk density, texture, and nutrient redistribution were not directly measured. Future studies combining controlled experiments and temporal observations are needed to clarify the mechanisms underlying these spatial patterns.

5. Conclusions

Our results showed that differences among BSC-associated soil categories were more pronounced for extractable nutrient fractions than for total nutrient pools in the adjacent 0–5 cm surface soil. Among total nutrients, only TN differed significantly among categories. In contrast, NO_3^- -N, NH_4^+ -N, extractable inorganic N, and NaHCO_3 -extractable P were highest in soil adjacent to moss crusts, whereas NH_4OAc -extractable K was lower in

bare sand than in both BSC-associated categories. Random forest and SEM analyses indicated that these nutrient patterns were associated with EC, TN, the site-level BSC metric, and regional environmental gradients. These findings characterize regional nutrient heterogeneity around BSC patches but do not establish causal relationships.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/soilsystems10080087/s1>, Figure S1: Permutation-based variable importance for random forest models of extractable nutrient fractions; Figure S2: Partial-dependence plots showing the modelled associations between the leading predictors and extractable nutrient fractions in the random forest models; Table S1: Random forest model performance and permutation-based variable importance for extractable nutrient fractions; Table S2: Complete Pearson correlation matrix among soil nutrients, environmental variables, geographic factors, and the site-level BSC metric.

Author Contributions: Conceptualization, Y.L. and H.Y.; methodology, Y.L., D.D., B.S., Z.F., W.X., W.H. and Y.G.; software, Y.G.; validation, Y.L., D.D., B.S., Z.F., W.X. and W.H.; formal analysis, Y.L., D.D., B.S., Z.F., W.X. and W.H.; investigation, Y.L., D.D., B.S., Z.F., W.X., W.H., X.S., X.T. and M.Y.; resources, Y.L. and H.Y.; data curation, Y.L., D.D., B.S., Z.F., W.X., W.H. and Y.G.; writing—original draft preparation, Y.L. and Y.G.; writing—review and editing, Y.L., D.D., B.S., Z.F., W.X., W.H., Y.G. and H.Y.; visualization, Y.L., D.D., B.S., Z.F. and Y.G.; supervision, Y.L. and H.Y.; project administration, Y.L. and H.Y.; funding acquisition, H.Y. All authors have read and agreed to the published version of the manuscript.

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