Postprint: Effects of Different Biological Soil Crust Types on Herbaceous Plant Diversity in the Gurbantünggüt Desert

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Abstract

We selected three different sampling sites in the northern (Site 1), central (Site 2), and southern (Site 3) parts of the Gurbantunggut Desert to compare the differences in herbaceous plant diversity and their main environmental influencing factors between bare sand and three types of biological soil crusts (algal crust, lichen crust, and moss crust). The results showed that: (1) The soil physicochemical properties differed significantly among different biological soil crust types. The contents of soil organic matter, total nitrogen, total phosphorus, total potassium, as well as clay, silt, and fine sand increased significantly with biological crust succession, while the contents of medium sand and coarse sand showed a significant decreasing trend. These properties exhibited obvious spatial heterogeneity across different regions of the desert. The nutrient contents and pH of bare sand and algal crusts at Site 2 were significantly lower than those at Site 1 and Site 3. (2) The species richness and Shannon-Wiener index of herbaceous plants showed a significant increasing trend with the development of biological soil crusts. The species composition and community structure of herbaceous plants differed significantly among different types of biological crusts and across different regions of the desert. (3) Among the soil physicochemical characteristics, the contents of organic matter, available P, and total K, as well as pH and silt content, were the key factors influencing the distribution of herbaceous plants. (4) The differences in microtopography and species composition among different types of biological soil crusts, seed biological characteristics, and soil environmental heterogeneity of biological crusts at different scales jointly influence the species composition and abundance of herbaceous plants in biological crusts, ultimately leading to successional changes in herbaceous plant community structure within biological crusts.

Full Text

Preamble

Effects of Different Biological Soil Crust Types on Herbaceous Plant Diversity in the Gurbantunggut Desert

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Abstract

This study investigated herbaceous plant diversity across three sampling sites in the Gurbantunggut Desert (northern, central, and southern regions), comparing bare sand with three biological soil crust (BSC) types: algal crust, lichen crust, and moss crust. The results revealed significant differences in soil physicochemical properties among BSC types. Soil organic matter, total nitrogen, total phosphorus, total potassium, and the contents of clay, silt, and fine sand increased significantly with BSC succession, while medium and coarse sand contents decreased markedly. Spatial heterogeneity was evident across desert regions, with Site 2 showing lower nutrient content and pH in bare sand and algal crusts compared to Sites 1 and 3. Herbaceous species richness and Shannon-Wiener diversity index increased significantly with BSC development. Both species composition and community structure varied significantly among BSC types and across desert regions. Among soil physicochemical characteristics, organic matter, available phosphorus, total potassium, pH, and silt content emerged as key factors influencing herbaceous plant distribution. The combined effects of microtopographical differences among BSC types, seed biological characteristics, and soil environmental heterogeneity at different scales collectively influence herbaceous species composition and abundance, ultimately driving community succession within BSCs.

Keywords: biological soil crusts; succession; herbaceous plants; species diversity; Gurbantunggut Desert

Introduction

Biological soil crusts (BSCs) are widely distributed in arid and semi-arid regions worldwide and constitute an important component of desert surface landscapes. These complex organic composites form through the cementation of cyanobacteria, eukaryotic algae, bacteria, fungi, lichens, mosses, and soil particles. BSCs enhance soil fertility through photosynthetic carbon fixation and nitrogen fixation, while effectively preventing wind and water erosion, conserving soil moisture, and promoting vegetation succession to stabilize ecosystems. In desert ecosystems, BSCs play irreplaceable ecological functions.

The succession from bare sand to mature moss crust is a complex process characterized by distinct dominant species at different developmental stages. Based on dominant species composition, BSCs are classified into three types: algal crust, lichen crust, and moss crust. Initially, bare sand consists of loose particles with no crust formation or only physical crusts. Microscopic observation and cultivation experiments confirm the colonization of filamentous cyanobacteria during this stage. Under suitable conditions, these cyanobacteria proliferate, with filamentous species binding loose sand particles through entanglement and adhesion to form algal crusts. Early algal crusts are dominated by filamentous cyanobacteria such as *Microcoleus vaginatus*, appearing light-colored. As development progresses, the crust darkens with increased heterocyst-forming nitrogen-fixing cyanobacteria and spherical cyanobacteria or green algae, forming dark algal crusts. In these advanced algal crusts, cyanobacteria or green algae can combine with fungi to form lichens, thickening the crust (1–2 cm) and increasing surface roughness, which develops into lichen crust. In interdune lowlands under shrubs, mosses begin to appear within some lichen crusts, gradually increasing in abundance and sometimes forming pure moss stands, representing the moss crust stage with thickness reaching 2–3 cm.

BSC development alters soil texture from coarse to fine, increases soil porosity, and enhances nutrient and salt content. These changes affect seed germination, seedling establishment, settlement, and survival of vascular plants, thereby influencing species diversity. In the Shapotou area and Horqin Sandy Land, BSC development increased seed bank density, with moss crusts showing significantly higher densities than algal crusts. However, in the Gurbantunggut Desert, algal crusts exhibited significantly higher seed quantity, richness, and diversity than lichen and moss crusts. For the same crust type, moist-treated crusts showed significantly higher seed bank density than dry-treated crusts. Soil seed banks serve as the material basis for vegetation regeneration and are closely related to plant diversity.

Further research indicates that dense BSC layers reduce seed plant diversity, while moderate disturbance of BSCs can increase plant diversity, though severe disturbance decreases it. Numerous studies have examined BSC effects on seed banks, with most concluding that BSC succession benefits seed bank density and diversity. However, whether herbaceous plant diversity responds similarly to different BSC types, and which soil environmental factors influence herbaceous plant diversity, remain unclear. To address these questions, this study investigates BSC succession effects on herbaceous plant diversity and key environmental factors in the Gurbantunggut Desert, enhancing our understanding of BSC-plant interactions.

1.1 Study Area Overview

The Gurbantunggut Desert, located in the Junggar Basin of Xinjiang (44°11 - 46°21 N, 84°31 -90°00 E), covers an area of 4.88×10^4 km^2 and represents China' s largest fixed and semi-fixed desert. The region experiences a typical temperate continental arid climate with relatively uniform seasonal precipitation distribution, annual precipitation of 70–150 mm, annual evaporation of 2000–2800 mm, and mean annual temperature of 5–5.7°C. Desert soils are primarily gray desert soils. The vegetation consists of small arboreal communities dominated by *Ephedra distachya*, *Haloxylon ammodendron*, *Haloxylon persicum*, and other psammophytes. Stable snow cover during winter provides abundant meltwater that facilitates BSC development and supports rich ephemeral plant communities. Additionally, well-developed BSCs exhibit strong selective distribution patterns across different dune geomorphological positions.

1.2 Methods

1.2.1 Field Sampling

In late April 2017, we conducted plant diversity surveys at three sites in the Gurbantunggut Desert separated by approximately 60 km: Site 1 (87°83 E, 45°06 N), Site 2 (87°61 E, 44°85 N), and Site 3 (88°24 E, 44°55 N). Annual precipitation at Sites 1, 2, and 3 was 76.26 mm, 109.72 mm, and 126.33 mm, respectively. At each site, we selected four crust types representing different successional stages: bare sand, algal crust, lichen crust, and moss crust. For each crust type, we randomly established 10 quadrats (1 m × 1 m). Using the grid method, we recorded plant species names, measured individual numbers, heights, and crown widths, and identified species using *Flora of China* and *Flora of Xinjiang*.

Soil samples were collected from each quadrat using a five-point sampling method for physicochemical analysis. Soil cores were taken at depths of 0–2 cm and 2–5 cm, mixed uniformly, sealed in plastic bags, transported to the laboratory, and air-dried under natural conditions before analysis.

1.2.2 Soil Physicochemical Property Measurements

Soil physicochemical properties were measured using standard methods: organic matter by potassium dichromate volumetric method; total nitrogen by Kjeldahl method; total phosphorus by acid dissolution-molybdenum antimony colorimetry; total potassium by flame photometry; available phosphorus by $NaHCO_3$ extraction-molybdenum antimony colorimetry; available nitrogen by alkali hydrolysis diffusion method; available potassium by atomic absorption spectrophotometry; pH using a pH meter in 1:5 soil-water suspension; total salts by gravimetric analysis after 20 mL extract drying. Soil particle size was determined using dry sieving combined with laser diffraction: coarse sand (>0.5 mm) and medium sand (0.2-0.5 mm) by dry sieving (sieve diameters 0.5 mm and 0.2 mm); fine sand (20–200 m), silt (2–20 m), and clay (<2 m) by laser diffraction.

1.2.3 Species Diversity Measurements

Species diversity was characterized by species richness (species number per unit area) and the Shannon-Wiener index. Dominant species were determined by importance value.

Shannon-Wiener diversity index:

$$H' = -\sum_{i=1}^{S} P_i \ln P_i$$

where S is total plant species number, N is total individual count, and P_i is the proportion of species i.

Importance value = (relative density + relative coverage + relative height)/3, with relative density, coverage, and height calculated using conventional methods.

1.2.4 Data Analysis

One-way ANOVA analyzed significant differences in soil properties and plant diversity indices among BSC types and sites. Significant differences were further examined using multiple comparison tests (LSD). Plant community structure differences were tested using PerMANOVA in SPSS 21.0. Canoco 5.0 analyzed relationships between plant community structure and environmental factors, with Mantel test identifying key environmental factors influencing community distribution. PASSaGE analyzed spatial heterogeneity of soil environmental factors among sites.

2.1 Effects of Different BSC Types on Soil Physicochemical Properties

Analysis of BSC physicochemical properties in the Gurbantunggut Desert revealed that succession facilitated organic matter accumulation and nutrient enrichment. In the crust layer, organic matter, total N, total P, available P, and available K contents increased significantly with BSC succession ($P < 0.01$), peaking in moss crusts. Total N showed no significant differences among successional stages ($P > 0.05$). Total salt content increased during succession, with lichen and moss crusts significantly higher than bare sand and algal crusts ($P < 0.01$). pH showed an initial increase followed by decrease, with algal and lichen crusts significantly higher than moss crusts ($P < 0.05$). Soil texture shifted from coarse to fine during succession, with clay, silt, and fine sand proportions increasing significantly ($P < 0.01$), while medium and coarse sand proportions decreased significantly ($P < 0.01$).

In the sub-crust layer (2–5 cm), organic matter increased slowly through the first three stages (bare sand, algal crust, lichen crust) without significant changes, but was significantly higher in moss crusts than other stages. NO_3^--N and NH_4^+-N contents increased significantly with succession ($P < 0.05$, $P < 0.01$), while total P and available P showed no significant differences among stages. Total salt and pH trends mirrored the crust layer but were slightly lower. Sub-crust particle size showed similar trends to the crust layer ($P < 0.01$).

2.2 Herbaceous Plant Diversity Index Analysis

Herbaceous species richness was significantly higher only in lichen crusts at Site 3 compared to other stages, with no significant differences at other sites. Across the desert, plant richness showed variation among sites: at central Site 2, lichen crust richness was lower than at western Site 1 and southern Site 3, while moss crust richness at Site 3 was significantly higher than at Sites 1 and 2. Shannon-Wiener index increased significantly with BSC succession at southern Site 3, but showed no significant differences among stages at western Sites 1 and 2. Across sites, Shannon-Wiener index was significantly higher at Site 3 than Site 1, while Site 2 showed no significant differences (Fig. 3).

2.3 BSC Plant Species Composition

The survey identified 15 species belonging to 9 genera in the Gurbantunggut Desert. Except for some bare sand quadrats, *Erodium oxyrrhynchum* and *Carex physodes* dominated all BSC successional stages. *Lappula semiglabra* and *Hyalea pulchella* dominated bare sand, with *E. oxyrrhynchum* dominance significantly lower in bare sand at Sites 1 and 3 compared to other BSC stages. *Alyssum linifolium* was a common dominant species in algal and lichen crust stages (Table 1).

Dominant species varied among sites separated by ~60 km. In bare sand, Site 2 was dominated by *E. oxyrrhynchum* and *H. pulchella*, while Sites 1 and 3 were dominated by *C. physodes*. In algal crusts, besides *E. oxyrrhynchum* and *C. physodes*, *A. linifolium* and *H. pulchella* showed clear dominance at Site 3 ($21.07\% \pm 22.87\%$ and $12.81\% \pm 9.27\%$, respectively), while Sites 1 and 2 were dominated by *Nepeta micrantha* and *H. pulchella* ($16.75\% \pm 11.86\%$ and $15.72\% \pm 11.77\%$, respectively). *Lappula semiglabra* individuals were not found in Site 2 quadrats. In lichen crusts, *A. linifolium* dominance at Site 3 was $20.99\% \pm 17.33\%$, significantly higher than at Site 1 ($6.06\% \pm 5.96\%$), while absent at Site 2.

2.4 Effects of BSC Type and Soil Physicochemical Properties on Herbaceous Community Structure

Canonical correspondence analysis explained 42.4% of cumulative variation, with the first and second axes explaining 13.63% and 9.62%, respectively. At small scales, BSC types influenced herbaceous community structure. Within sites, different crust types generally showed distinct plant communities, though some overlap occurred: at Site 2, lichen and moss crust communities were similar, and at Site 3, algal and lichen crust communities overlapped, indicating species mixing within BSC quadrats. At the 60 km scale, the same crust type showed significant differences among sites, with plant communities differing significantly between sites for most crust types.

PerMANOVA revealed that BSC type had highly significant effects on plant community structure ($P < 0.01$). Bare sand communities differed significantly or highly significantly from lichen and moss crusts at all three sites. Additionally, algal crusts differed significantly from lichen and moss crusts at Site 1, while bare sand differed significantly from algal crusts at Sites 2 and 3 ($P < 0.05$ or $P < 0.01$). Desert sites also differed significantly: algal and lichen crust communities at Site 1 differed significantly from those at Sites 2 and 3, mostly at highly significant levels ($P < 0.01$). Similarly, Sites 2 and 3 differed significantly for most crust types ($P < 0.05$).

Mantel test analysis showed that bare sand communities correlated positively with medium sand (0.2–0.5 mm) and coarse sand (>0.5 mm). Algal and lichen crust communities correlated positively with organic matter and total N, while moss crust communities showed significant positive correlations with NO_3^--N, NH_4^+-N, silt, clay, and fine sand contents (Fig. 4). Plant communities in different successional stages correlated significantly with available phosphorus ($r = 0.283$, $P = 0.001$) and silt ($r = 0.251$, $P = 0.009$), but negatively with organic matter ($r = -0.143$, $P = 0.046$) and total K ($r = -0.141$, $P = 0.038$), indicating that soil nutrients, pH, and texture comprehensively influence plant communities.

3 Discussion

3.1 Effects of BSC Microtopography and Seed Biological Characteristics on Plant Diversity

This study revealed significant differences in plant species composition and dominance across BSC successional stages. *Lappula semiglabra* occurred only in bare sand as a dominant species. *Hyalea pulchella* dominance was significantly higher in bare sand and algal crusts than in lichen and moss crusts. *Erodium oxyrrhynchum* dominance in bare sand at Sites 1 and 3 was significantly lower than in other BSC stages. *Alyssum linifolium* was a common dominant in algal and lichen crusts, while *Ephedra distachya* was a dominant indicator species in moss crusts. These changes likely relate to microenvironmental alterations during BSC succession and seed biological characteristics.

BSC development modifies soil surface microtopography. Bare sand consists of loose particles with smooth surfaces. Algal crusts develop fine cracks that provide microsites for small seed colonization. Lichen crusts increase surface roughness substantially, with seeds more easily lodging in depressions, enhancing seed-soil contact and potentially improving water absorption and germination. Moss crusts exist as patchy aggregations that create physical barriers for seed contact with soil, inhibiting germination and establishment. Experimental studies confirm that moss crusts significantly inhibit germination of some desert plant seeds, including *Haloxylon ammodendron*, *Salsola subcrassa*, *Ceratoides ewersmanniana*, and *Ceratocarpus arenarius.

Different BSC microtopographies selectively filter seeds of different sizes and morphologies. *Lappula semiglabra* seeds have small tuberculate protuberances and short spines on the central back, with hard seed coats that facilitate fixation on bare sand surfaces and promote germination under suitable conditions. *Erodium oxyrrhynchum* propagules have cone-shaped structures with awns, bristles, and villi attachments. The awn base contains a spiral structure that unwinds under humid conditions, enabling penetration through BSCs for successful establishment while being protected by the microenvironment. This specialized morphology explains its dominance across most BSC types. *Carex physodes* fruits have bladder-like utricles and *Hyalea pulchella* fruits have pappus, both adapted for wind dispersal, resulting in relatively uniform distribution across different BSC microtopographies.

Seed biological characteristics also influence diversity patterns. *Carex physodes* seeds exhibit dormancy, with cold storage significantly enhancing germination rates. Different snow cover depths during winter may affect soil temperature, influencing dormancy release and germination. *Alyssum linifolium* propagules show mucilage phenomena with sand-adhering capacity, an effective adaptation for reducing displacement in sandy or arid environments. Dense moss layers in moss crusts create physical barriers that block seed-soil contact and compete intensely for water, making it difficult for seeds to obtain sufficient moisture for germination, thereby reducing species number and individuals. The dominance of *Ephedra distachya* in moss crust quadrats relates to its close association with the dominant moss *Didymodon vinealis*, as *E. distachya* provides shade and rainwater concentration, creating suitable habitats for moss growth.

3.2 Effects of BSC Development on Plant Diversity

This study found significant differences in plant community structure among BSC types, with herbaceous diversity varying by crust type. At Sites 1 and 3, herbaceous and semi-shrub richness increased gradually with BSC succession, peaking in lichen crusts but declining in moss crusts. At Site 3, Shannon-Wiener index increased significantly during succession, closely related to species composition changes. Bare sand had low microbial abundance and nutrient deficiency, supporting fewer plants dominated by 贫瘠-tolerant ephemerals such as *E. oxyrrhynchum*, *C. physodes*, *L. semiglabra*, *A. linifolium*, and *H. pulchella*. Algal crust formation increased cyanobacteria, eukaryotic algae, and other photosynthetic microorganisms, enhancing soil organic carbon and key nutrients for desert surface soils. Lichen crust development further increased photosynthetic capacity through lichen and algal components, accumulating more carbon while nitrogen-fixing microorganisms enriched soil nitrogen. Bacterial and fungal biomass increased significantly during succession, with heterotrophic microorganisms mineralizing organic matter to increase nutrient availability. This gradual nutrient accumulation provides essential conditions for vascular plant survival and growth, directly affecting seed dispersal, germination, and nutrient absorption.

Previous studies found that BSCs significantly enhanced N, P, and K uptake in *E. oxyrrhynchum*, *A. linifolium*, and *H. pulchella*, but not Ca and Mg uptake. BSC organic carbon accumulation promotes soil microbial activity and enzyme function, providing available nutrients for plant germination and growth through mineralization. Forest ecosystem research indicates that alkali-hydrolyzable nitrogen and available phosphorus are directly utilizable nutrients that positively correlate with plant diversity. In this study, soil organic matter, total N, available P, and available K increased significantly with BSC succession, providing valuable nutrient conditions for vascular plants. However, excessive nutrient accumulation may inhibit plant diversity, as indicated by the negative correlation between NH_4^+-N and species richness, suggesting NH_4^+-N plays a key role in plant growth regulation.

3.3 Effects of Soil Environmental Heterogeneity at Different Scales on Plant Diversity

BSC plant communities showed significant or highly significant differences among sites separated by ~60 km. Mantel test analysis revealed significant correlations between plant communities and organic matter, available P, total K, and silt content, indicating comprehensive influences of soil nutrients, pH, and texture. PASSaGE analysis of soil physicochemical characteristics showed significant differences among sites, particularly between Site 3 and Sites 1-2, with the first two axes explaining 53.51% and 16.17% of total variation, respectively. This soil spatial heterogeneity affects nutrient supply, influencing plant species composition and abundance and causing significant community structure changes.

In the Gurbantunggut Desert, soil organic matter, NH_4^+-N, available P content differences, and BSC development create microhabitat heterogeneity. Total K, available K, and electrical conductivity correlate positively with species richness in *Ephedra distachya*, *Seriphidium terrae-albae*, and *Artemisia desertorum* communities, while pH correlates negatively, confirming soil heterogeneity effects on plant diversity. BSCs also influence *Artemisia ordosica* community diversity. In moderately and severely degraded grasslands of the Qilian Mountains, NH_4^+-N, organic matter, and available K positively correlate with vegetation biomass. In this study, Site 2 had lower nutrient content in bare sand and algal crusts than Sites 1 and 3, and lower available K and NH_4^+-N in lichen crusts. Site 3 had significantly higher available P, silt, and clay contents in bare sand. These differences in soil nutrients and texture created significant environmental heterogeneity, providing diverse habitats that affected herbaceous species composition and community structure.

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4 Conclusion

In the Gurbantunggut Desert, different BSC types influence herbaceous species composition and community structure. *Erodium oxyrrhynchum* and *Carex physodes* dominated all BSC types. Plant communities differed significantly or highly significantly between algal crusts and other crust types. Microtopographical differences among BSC types, seed biological characteristics, and soil environmental heterogeneity at different scales collectively influence herbaceous species composition and abundance, driving community succession. Soil organic matter, available P, total K, pH, and silt content are key soil physicochemical factors affecting plant community structure in BSCs.

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Note: Figure translations are in progress. See original paper for figures.