Hillslope Geodiversity Impact on Biocrusts’ Biogeochemical Functions

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Abstract: Geodiversity integrates physical parameters such as geological, geomorphological, and pedological components. It represents the abiotic diversity of the earth surface layer. It incorporates geological (bedrocks and mineral sediments), geomorphological (geography, land surface formations, physical processes), pedological (soils), and hydrological characteristics. Biological soil crusts (biocrusts) play an essential role in regulating the biogeochemical cycles of carbon and nitrogen. Their ability is dependent on habitat conditions, composition, and cover percentage of the ground surface, all of which are affected by geodiversity. This study’s objective was to assess the effects of geodiversity on the biogeochemical functions of biocrusts by regulating the soil water dynamics and the subsequent impact on readily available nitrogen and carbon. Hillslope geodiversity is determined by the geodiversity found in the stone cover on the ground surface and in the stone content throughout the soil profile, as well as by the soil profile thickness of the underlying bedrock. We hypothesized that in dry environments, the physical conditions in high-geodiversity hillslopes, compared to low-geodiversity hillslopes, positively affect the soil water budget, which would affect the biocrusts and their readily available nitrogen and carbon. The results showed higher soil moisture content in the heterogeneous hillslopes. The ammonium and labile organic carbon in the biocrusts were more substantial in the heterogeneous than in the homogeneous hillslopes, while soil protein, nitrite, and soil organic matter were similar. We suggest that the comparatively high soil moisture content in the heterogeneous hillslopes stimulates biocrust community activities and increases the readily available nitrogen and carbon, thus improving the survival of shrubs in these ecosystems under long-term drought conditions.

Keywords: biogeochemical cycles; bio-geodiversity; biological soil crusts; stoniness; N-NH4; labile organic carbon

1. Introduction

Geodiversity integrates physical parameters such as geological, geomorphological, and pedological components [1]. It incorporates geological (bedrocks and mineral sediments), geomorphological (geography, land surface formations, physical processes), pedological (soils), and hydrological characteristics [1]. Geodiversity enhances the development of multiple ecological niches, and, either directly or indirectly, sustains biodiversity under various climatic conditions [2–8]. It has been suggested that high geodiversity
increases vegetation survivability in ecosystems; therefore, these systems are more resilient under climatic change scenarios, such as consequent and prolonged drought years [9]. Recent studies in the semiarid northwestern Negev of Israel showed that hillslope geodiversity, characterized by stony soil surface and shallow depth, positively affects soil water availability for perennial vegetation, increasing chances of survival under low rainfall regimes and drought conditions [10–12].

Biogeochemical cycles of carbon and nitrogen in dryland soils, where wetting events and vegetation are scarce, are substantially regulated by biological soil crusts (biocrusts) [13–16]. Biocrusts occupy the soil surface’s upper layer (~10 mm) and encompass diverse communities composed of cyanobacteria, lichens, mosses, fungi, and other microbes that live in the crust sphere in the soil. Biocrusts contribute to soil quality and fertility by increasing the organic carbon content and by fixing atmospheric carbon and nitrogen [17–19]. Biocrusts’ ability to play a role in biogeochemical cycles depends on their habitat conditions, the availability of soil moisture following rain events [19], cover percentage, surface roughness, soil infiltrability, and microbial composition, all of which are affected by the soil type [20–23].

In spite of recent studies, the mechanisms through which biocrust cover is affected by geodiversity [23] are still not fully understood. Specifically, the effects of hillslope geodiversity on biocrusts’ biogeochemical function by regulating the soil water dynamics and the subsequent impact on readily available nitrogen and carbon, are still unknown.

The study objective was to assess the effects of hillslope geodiversity on biocrusts’ biogeochemical function by regulating soil moisture content. We hypothesized that in dry environments, the physical conditions in high-geodiversity hillslopes, compared to low-geodiversity hillslopes, positively affect the soil water budget. Through regulating the soil water dynamics, differences in geodiversity settings between homogeneous and heterogeneous hillslopes, which are determined by the stone cover on the ground surface and in the soil profile, as well as by the soil thickness, affect the biocrusts and their readily available nitrogen and carbon.

2. Materials and Methods
2.1. The Study Sites

The northwestern Negev is characterized by a semiarid climate, with a long-term average rainfall of 200 mm annually, which falls between November and March. This amount of rain has significantly decreased in recent years and currently measures ~150 mm a year. Average daily minimum temperatures in winter are 6–8 °C, and average daily maximum temperatures in summer are 32–34 °C [24]. The region’s soil is characterized as sandy loam Calcixerolic or Xerochrepts (USDA classification) and comprises 14% clay, 27% silt, and 59% sand, which overlays Eocene bedrock [23,25]. The study was conducted in the Sayeret Shaked Park Long-Term Ecological Research (LTER) site, located in the northern Negev (31°17’ N; 34°37’ E; 185 m.a.s.l.) (Figure 1). The characterizing ground cover is a mosaic of biocrust and small patches of dwarf shrubs, mainly *Noaea mucronata, Atractylis comosa* and *Thymelaea hirsute* [26].
Figure 1. A satellite image of Israel (A), with an enlarged aerial photograph of the study area at the Sayeret Shaked Park LTER site (B), indicating the sampled homogeneous (green) and heterogeneous (blue) hillslopes.

2.2. Field and Laboratory Work

The Shaked Park LTER site’s biocrust community is well documented in previous works [25,27–29]. We used remote sensing images from LANDSAT 2 (pixel size of 10 m, and revisit time of 10 days) to determine the soil moisture content in hillslopes according to the optical trapezoid model (OPTRAM) [30]. The OPTRAM includes four computation steps: (a) transformed reflectance computation; (b) calculation of the normalized difference vegetation index (NDVI); (c) estimation of the minimal and maximal borders using quantile regression of the transformed reflectance; (d) calculation of the OPTRAM using the normalization of transformed reflectance by the minimal and maximal borders (Equation (1)):

$$\text{OPTRAM}_i = \frac{r_{\text{max},i} - r_i}{r_{\text{max},i} - r_{\text{min},i}}$$  \hspace{1cm} (1)

where $r_{\text{max},i}$ and $r_{\text{min},i}$ are the maximum and minimum of the transformed reflectance $r_i$ (for more details on the OPTRAM calculation and field validation, see [31]).

The effects of hillslope bio-geodiversity on the nitrogen and carbon readily available in biocrusts were investigated in three homogeneous and three heterogeneous hillslopes. We monitored the ground surface in two 25 m transects (Figure 2a,c) in the six hillslopes (three of each type), where the hillslopes were regarded as statistical plots [23]. Duplicate biocrust samples were collected every 5 m along each transect. The biocrust samples (64 cm$^2$, $n = 60$) were carefully collected during the dry season from a depth of 1–2 cm and transferred to the laboratory for analysis.
Figure 2. Biocrust sampling in a heterogeneous (high-geodiversity) hillslope, with a high cover of shrubs and stones (a); dark-colored biocrust from a heterogeneous hillslope (b); biocrust sampling from a homogeneous (low-geodiversity) hillslope, with low woody vegetation cover and negligible stone cover (c); light-colored biocrusts from a homogeneous hillslope (d).

The biocrust samples were sieved (<2.0 mm) to remove small stones and plant debris. The inorganic nitrogen concentrations were determined by extracting the biocrust samples using 1 M KCl (2.5 g in 10 mL, 60 min) and filtering them through 0.45 µm filters. Soil ammonium nitrogen (N-NH₄) was measured after extraction using the Nessler method and using colorimetric analysis with Nessler’s reagent at a wavelength of 420 nm [32]. The colorimetric analysis with a diazotizing reagent was used to measure soil nitrate nitrogen (N-NO₃) after biocrust extraction, at a wavelength of 543 nm [33]. The concentration of ammonium nitrogen (N-NH₄) and nitrite nitrogen (N-NO₂) was calculated according to Equation (2):

\[
\frac{N-(NO₂)}{N-(NH₄)} = (A \text{ sample}) \times 4
\]

where “A sample” represents the nitrogen concentration in the sample after multiplying by the regression value of the calibration curve, and 4 is the dilution factor.

The SOM content was determined by combustion at 450 °C [34]. The Labile Organic Carbon (LOC) was measured following Tirol-Padre et al. (2004) [35] at a wavelength of 550 nm. The amount of LOC in the sample was calculated according to Equation (3):

\[
LOC(\text{mg g}^{-1}) = \frac{(A \text{ Sample}) \times (50/2) \times 25 \times 9}{1000 \text{ (mL L}^{-1}) \times \text{ wt of sample (g)}}
\]

where “A sample” comprises the KMnO₄ solution concentration in the sample after multiplying the spectrophotometer reading by the regression value of the calibration curve; 50/2 is the dilution factor; 25 is the volume (in mL) of the KMnO₄ solution added to the soil sample; finally, 9 is the amount of carbon dioxide for each mol KMnO₄. The Lowry method, with 0.1 N NaOH [36], was used to determine the protein content.

The types of soil surface cover (dark in color for cyanobacteria, moss, and lichen crust community, and light in color for cyanobacterial biocrust), according to hillslope-type, were visually estimated within the 25 cm² quadrats, along the two 25 m transects along the six hillslopes [37], with a total of 150 for each hillslope type.
2.3. Statistical Analysis

Statistical analyses were performed using JMP 14.0 (JMP Developers, 100 SAS Campus Drive Cary, NC 27513. US.). The effects of the hillslope type (homogeneous vs. heterogeneous) on the biocrusts' parameters, i.e., protein, N-NO₂, N-NH₄, SOM, and LOC, were determined through t-tests, using JMP version 14.0 [38].

3. Results

The soil moisture content was higher in the heterogeneous hillslopes than in the homogeneous ones throughout the two-year sequence, except for the short transition period between late spring (April) and the beginning of the summer season (May) (Figure 3). The content of SOM, LOC, and N-NH₄ in the heterogeneous hillslopes was higher than in the homogeneous hillslopes (p < 0.0001, p = 0.0235, p < 0.0001, respectively). No significant differences were recorded for protein and N-NO₂ (p = 0.928 and p = 0.362, respectively) (Table 1).

Table 1. Carbon and nitrogen parameters of biocrusts according to the hillslope type.

<table>
<thead>
<tr>
<th>Hillslope Types</th>
<th>SOM (g kg⁻¹)</th>
<th>LOC (mg g⁻¹)</th>
<th>N-NH₄ (mg kg soil⁻¹)</th>
<th>N-NO₂ (mg kg soil⁻¹)</th>
<th>Protein (mg kg⁻¹ soil⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heterogeneous</td>
<td>4.632 (±0.756 *) a</td>
<td>0.00715 (±0.0030) a</td>
<td>2.536 (±1.685) a</td>
<td>0.112 (±0.079) a</td>
<td>0.0917 (±0.041) a</td>
</tr>
<tr>
<td>Homogeneous</td>
<td>3.949 (±0.778) b</td>
<td>0.00626 (±0.0022) b</td>
<td>1.659 (±0.882) b</td>
<td>0.102 (±0.069) a</td>
<td>0.0912 (±0.034) a</td>
</tr>
</tbody>
</table>

* The numbers in brackets indicate the standard deviation. Different letters in the same column indicate a statistical difference between the heterogeneous and homogeneous hillslopes.

4. Discussion

The soil moisture content is primarily determined by the rainfall regime and has great significance in dryland environments [19]. Hjort et al. (2015) [5] suggested that geo-diversity influences biodiversity by determining the heterogeneity of the physical environment in interactions with precipitation. Similarly, Stein et al. (2014) [3] reported that heterogeneity in land cover, vegetation, climate, and soil and topography are significantly positive on different scales. In this study, geo-diversity was found to determine the difference in soil moisture content between the two hillslope types (Figure 3, Table 1). In turn, the soil moisture content regulates the biocrust communities in the two hillslope types (Figure 4a).

The biocrusts' development and structure are, therefore, mainly regulated by the soil moisture as a result of the rainfall regime, their soil properties and distribution, and the quantity that determines the infiltration rate (Figure 4b) [7,8,29,39]. The soil moisture content determines the biocrust community’s growth rates, biocrust composition, duration of activities, and successional development stage, and their distribution in dry environments is predominantly based on gradual climatic gradients [40,41]. Biocrust organisms are affected and activated physiologically when the soil is wet, and soil moisture is essential for C and N fixation. Our findings show that high geo-diversity increases soil moisture; therefore, biocrust distribution and its development and activity would be primarily affected by the degree of heterogeneity of the geo-diversity. Barger et al. (2016) [18] compared N fixation rates for different biocrust types and in different seasonality. They reported that N-fixing cyanobacteria are the dominant N fixer in biocrusts. A mix of cyanobacteria species — *Nostoc* spp., *Tolypothrix* spp., and *Scytonema* spp. — revealed an average three to four times higher rate than light biocrusts and were four times higher than moss biocrusts. Moreover, during autumn and winter, late successional biocrusts (long-term and well-grown) were ten to five times higher than early successional (newly grown) biocrusts [18]. Zaady et al. (2000) [42] reported that early successional biocrusts from highly disturbed and dry areas, dominated by algae of cyanobacteria, show lower C-fixation values than those from undisturbed sites with higher soil moisture where lichens and mosses occur. Housman et al. (2006) [43] reported that later and dark successional biocrusts, dominated
by the cyanobacteria *Nostoc* spp. and *Scytonema* spp., and lichens *Placidium* spp. and *Col-lem* spp., typically had higher daily C fixation than early light successional biocrusts with filamentous cyanobacteria *Microcoleus vaginatus*. Recent studies have suggested that hillslope geodiversity increases ecosystem tolerance to droughts [7,10,11,31,44]. Zaady et al. (2021) [12] highlighted the effects of hillslope geodiversity on the properties and composition of biocrusts (Figure 5A). They suggested that hillslope geodiversity significantly affects biocrusts’ bio-physiological properties, and that high geodiversity enhances biocrust communities that require relatively higher soil moisture content. Moreover, in the high-geodiversity plots, the biocrust community was found to be darker and more affluent than that in the low-geodiversity settings (Figure 2b,d).

![Figure 3. Soil moisture content (SMC); OPTRAM method calculated from Equation (1) (see Dubinin et al., 2021 [44] for details) for a five-year sequence between 2018 and 2022 (each series comprises an average of three plots). The points represent the OPTRAM calculation and the curves represent the moving averages using Sentinel-2 imagery. The results emphasize the impact of geodiversity on SMC. The multiyear-mean SMC in the hillslopes with a high geodiversity is about 19%, while the multiyear-mean SMC in the hillslopes with a low geodiversity is about 17% (a). The difference in the SMC between the hillslopes is higher in the rainy season (*p* < 0.0009) (b).](image)

![Figure 4. Ground surface cover of heterogeneous and homogeneous hillslopes (a). The differences between the infiltration rate of the water between the two heterogeneous and homogeneous hillslopes (b).](image)
Figure 5. Biocrust communities’ cover in homogenous (low-geodiversity) and heterogeneous (high-geodiversity) hillslopes [23] (A); a conceptual model demonstrates the effects of geodiversity on soil moisture content and their impact on biocrusts, with consequences for readily available nitrogen and carbon, which increases shrubs’ resistance to droughts (B).

Using remote sensing images from LANDSAT 2 allowed us to determine the soil moisture content in the heterogeneous and homogeneous hillslopes (Figure 3). Overall, the heterogeneous hillslopes showed higher soil moisture content. A similar trend was reported for a five-year sequence (2013–2018) for the very same study site [7,31,44]. High soil moisture content in the heterogeneous hillslopes increases biocrust component activities such as available nitrogen and carbon (Figure 5B) [16,18,23,45]. The results for the organic matter can be explained by the possibly longer and higher activity of the biocrusts, which benefit from the higher soil moisture content.

Szitenberg et al. (2021) [46] reported a slight but consistent difference in the microbial community compositions between the homogeneous and heterogeneous hillslopes. They suggested that more ammonia-oxidizing and reducing carbohydrates bacteria existed in the homogeneous hillslopes, possibly decreasing the ammonia. The activities of the biocrust microbiome may explain the readily available nitrogen (N-NH4) by N fixation (cyanobacteria and free-living N-fixing bacteria) or the decomposition of the organic nitrogen compound aboveground and within the biocrust layer [18,45]. Sancho et al. (2016) [15] evaluated the contribution of biocrusts to the global terrestrial carbon cycle. The available LOC is a result of the decomposition of sugar, amino acids, peptides, amino sugars, and lipids [35]. The higher soil moisture content in the heterogeneous hillslopes compared to that in the homogeneous hillslopes might contribute to the higher concentration of readily available resources in the biocrust layer. Couradeau et al. (2019) [47] reported that the cyanobacteria Microcoleus vaginatus, which is very common in our study region [28], shows high microbiome activity in its cyanosphere, including N fixation and C exchange. Moreira-Grez et al. (2019) [48] showed that the microbial community composition depends on the biocrust type and is likely a product of the synergies between their populations. The biocrust type also plays a role in revealing the potential of N-fixing organisms, which consequently affects their C and N content. Nejidat et al. (2016) [29] suggested that heterotroph organisms depend on the N and C content provided by the phototrophic...
microorganisms. The activity of these microorganisms is highly controlled by the soil moisture content [16,18,39]. The N-NO\textsubscript{2} is subjected to transport with the soil solution. This may explain that despite a minor increase (Table 1), no significant differences were found in the N-NO\textsubscript{2} concentration between the two hillslope types.

The protein compounds in the soil originate from the entire population that makes up the biocrust community. These include the phototropic and heterotrophic organisms, as well as other soil organisms which probably exist in both hillslope types. Therefore, no significant differences were found between the low- and high-geodiversity hillslopes regarding the protein content (Table 1).

A conceptual model (Figure 5B) demonstrates the effects of geodiversity on the biocrust’s properties and its available resources. Changes in the soil moisture content affect the biocrust community’s structure and, consequently, the differences in its productivity and biogeochemical cycles. Depending on the soil moisture content levels, the more developed biocrust populations play a role in N fixation and in the potential activity of decomposer organisms, which consequently might affect the C and N contents and the availability of N-NH\textsubscript{4} and LOC. The higher soil moisture content in the heterogeneous hillslopes throughout the year makes N and C readily available, better sustaining the survivability of shrubs (Figure 2a) during consecutive drought years [49]. At the same time, shrubs on homogeneous hillslopes are less resistant to droughts (Figure 2c) [10,29,46] mainly due to the lower soil moisture.

5. Conclusions

In dry environments, geodiversity impacts the biogeochemical functions of biocrusts by regulating the soil moisture budget and determining the development of the biocrust community and affects the biocrusts and their readily available nitrogen and carbon. Heterogeneous hillslopes, with higher soil moisture content, benefit from greater cycling of the SOM and readily available LOC of biocrusts, and from N fixation in the heterogeneous hillslopes. This study highlights the important role played by biocrust community and its interaction with geodiversity in determining soil quality and functioning in dryland ecosystems.


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References


