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Impact of Soil Biological Crusts on the Sustainability of Arid Ecosystems in Central-Western Argentina: Their Influence on Nutrient Dynamics and Soil Properties

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Abstract: Biological soil crusts (BSCs) are common in arid and semi-arid regions, found in vegetation patches and interpatches. However, their distribution, functionality, and composition studies are limited, especially in South America and Argentina. This study assessed the functional differences in BSCs between patches and interpatches focusing on their role as fertility islands. Sixty plots were analyzed at two sites, measuring the soil's composition, diversity, and physical and chemical properties, including stability, compaction, temperature, moisture, nitrogen, phosphorus, organic matter, electrical conductivity, and pH. The results showed similar BSC coverage in patches and interpatches but with compositional variations: mosses dominated patches, while cyanobacteria and lichens were more common in interpatches. BSCs enhance soil stability, moisture retention, nitrogen fixation, and phosphorus availability, which are essential for soil health and ecosystem functionality. The observed variations across microenvironments are crucial for sustainability. Understanding these dynamics is vital for managing arid ecosystems, as healthy BSCs mitigate erosion, improve nutrient cycling, and enhance resilience to climate change. Preserving and managing BSCs composition and distribution are essential for the sustainability of these ecosystems in the region.

Keywords: fertility islands; interpatches; microhabitats; patches; soil stability

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Citation: Navas Romero, A.L.; Herrera Moratta, M.A.; Fernández-Maldonado, V.; Martínez Carretero, E.; Mazza, G.; Rodriguez, R. Impact of Soil Biological Crusts on the Sustainability of Arid Ecosystems in Central-Western Argentina: Their Influence on Nutrient Dynamics and Soil Properties. *Sustainability* **2024**, *16*, 10468. https://doi.org/10.3390/su162310468

Academic Editor: Anna De Marco

Received: 12 October 2024
Revised: 23 November 2024
Accepted: 27 November 2024
Published: 29 November 2024

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1. Introduction

Biological soil crusts (BSCs), complex microbial communities that colonize the Earth's surface, represent a crucial biological cover for the sustainability of dryland ecosystems [1]. They vary in composition and structure depending on local environmental conditions [2]. This diverse ecosystem comprises everything from cyanobacteria to lichens and mosses, which group together to form a cohesive matrix capable of influencing a variety of key ecological processes [2]. Their ability to stabilize soil, improve fertility, retain water, and promote biodiversity makes them critical components for the health and resilience of these fragile environments [3–5]. Protecting and promoting BSCs is essential to maintaining the sustainability of desert ecosystems.

Despite the attention devoted to BSCs in various studies, significant gaps remain in the understanding of their interactions with the surrounding environment, especially in arid environments and heterogeneous landscapes such as those in Argentina and South

America. These arid environments, characterized by low rainfall and low nutrient concentration, present unique challenges for plant and microbial life [6]. In this context, the presence of BSC communities, even in a small proportion of the soil profile, is essential to maintain fundamental ecological processes [7]. BSCs not only play a crucial role in regulating biogeochemical cycles and soil stability but are also critical for sustainability, particularly in arid ecosystems. By enhancing water and nutrient retention, they contribute to ecosystem resilience to disturbances and climate change. Finally, their ability to foster biodiversity and soil productivity makes them vital components for the sustainability of these environments [8].

Arid ecosystems show a special fragility to disturbances and lack of water and nutrients [9]. Furthermore, soil nutrient distribution in semiarid areas is concentrated under the plant canopy [10], while BSCs occupy the nutrient-poor areas surrounding vegetation patches, called interpatches [11]. Arid and semi-arid agrosystems, like those in central-western Argentina, are dominated by drought-tolerant vegetation such as *Larrea cuneifolia* Cav (creosote bush), *Zuccagnia punctata* Cav (jarilla), and *Prosopis flexuosa* (algarrobo), which play essential roles in soil stabilization, erosion control, and nutrient cycling [12,13]. These species interact closely with biological soil crusts (BSCs), particularly in interpatch areas, where BSCs enhance soil fertility, water retention, and aggregate stability, facilitating plant establishment in resource-limited environments [14].

Thus, most of the nutrient inputs and losses in the spaces between plants could be regulated by them [15]. The distribution of BSCs over a large part of the Earth's surface, mainly in the open spaces surrounding vegetation patches, allows them to participate in key ecosystem functions, increasing their potential [7].

As mentioned above, the spatial distribution of BSCs can vary within the same ecosystem, with formations present both in vegetation patches and interpatches [11,16]. This spatial differentiation may have important implications for the function and ecological role of BSCs in these environments. It has been suggested that BSCs located under vegetation patches experience different microclimatic conditions and nutrient fluxes compared to those located in interpatches [17,18]. However, understanding of the functional differences between these two specific locations remains limited. The distinction between vegetation patches and interpatches as distinct habitats for BSCs raises questions about the relative importance of these microenvironments in ecosystem dynamics and their role in their sustainability since the interaction between these spaces can influence the availability of resources and resilience to environmental changes. Furthermore, the possibility that BSCs present in interpatches act as "fertility islands", that is, areas of enriched soil that promote plant growth, is an aspect that has received increasing attention in the scientific literature [19]. This growing interest stems from the critical roles BSCs play in ecosystem functioning, particularly in arid and semi-arid environments where soil fertility and stability are naturally limited. BSCs enhance nutrient availability by fixing atmospheric nitrogen, trapping organic matter, and altering soil pH to create conditions favorable for plant establishment [14]. Additionally, their ability to reduce erosion and increase water retention makes them valuable for land restoration projects, especially in regions experiencing desertification and the impacts of climate change [8,14,16]. These practical applications have been recognized as key components in sustainable land management and ecological restoration efforts in dryland ecosystems worldwide. This interaction is especially relevant for agriculture and environmental restoration. In agriculture, BSCs improve soil fertility, reduce erosion, and enhance the establishment of crops and native plants by creating nutrient-rich microhabitats [14,20]. For restoration efforts, BSCs act as 'fertility islands', stabilizing degraded soils and promoting vegetation recovery, making them integral to combating desertification and ensuring ecosystem resilience [3,21]. Understanding these dynamics can inform sustainable land management practices and restoration strategies in arid regions like central-western Argentina.

In South America, biocrusts are widely distributed in arid and semi-arid lands, particularly in regions like central-western Argentina, where they play an essential role in

ecological processes [14,22]. However, studies about biocrusts in South America remain limited compared to the extensive research conducted in North America, Australia, and Europe [23,24]. Recent studies in Argentina have focused on the impact of disturbances on biocrusts and their effects on vascular plant germination, as well as their spatial distribution in regions like the Monte Desert [25,26]. These studies highlight the importance of biocrusts in nutrient cycling, soil stabilization, and biodiversity maintenance, emphasizing the need for more comprehensive research in these ecosystems.

This study contributes a novel perspective by focusing on the functional differences in biological soil crusts (BSCs) within vegetation patches and interpatches in central-western Argentina, a region underrepresented in biocrust research. Unlike previous studies that predominantly address the spatial distribution or impacts of disturbances on BSCs, this work integrates a comprehensive evaluation of biodiversity, soil properties, and their interactions to reveal the ecological roles of BSCs as 'fertility islands' in arid landscapes [22,25,26]. By highlighting the dual role of BSCs in nutrient-poor interpatches and under-plant canopies, this study provides insights that have not been extensively explored in arid and semi-arid ecosystems, particularly in South America. These findings fill a critical knowledge gap and establish a foundation for future research and practical applications in sustainable land management and ecological restoration.

Correlating and measuring soil nutrients, soil characteristics, and soil chemistry with biocrust community composition presents significant challenges due to the complexity of interactions and spatial variability inherent in these environments [27,28]. Spatial heterogeneity in soils, influenced by factors such as texture, structure, and organic matter content, can affect biocrust distribution and composition, complicating the identification of clear patterns [29]. Additionally, interactions between biocrusts and vascular plants, which can be competitive or facilitative, add another layer of complexity to studying these relationships [30]. Microclimatic conditions such as temperature and moisture also influence biocrust activity and composition, further complicating the correlation of these variables with community composition [31]. Therefore, multidisciplinary approaches and long-term studies are needed to unravel these complex interactions and improve our understanding of biocrusts in South America's arid ecosystems.

Moreover, sampling soil nutrients in such heterogeneous environments is methodologically complex. Nutrient concentrations often vary across microhabitats, with higher concentrations under plant canopies compared to interpatches dominated by biocrusts [22]. Microclimatic factors such as temperature and moisture also play a critical role, as they influence organic matter decomposition and nutrient cycling [32,33]. These dynamic and interacting factors require advanced sampling strategies and analytical approaches to accurately capture the complex relationships between soil properties and biocrust communities.

Despite the global recognition of the importance of biological soil crusts (BSCs) [8,34,35], few studies have explored their impact on arid systems in Argentina [10,16,26,36–38]. This study aims to assess the functional differences in BSCs between vegetation patches and interpatches, with a focus on their potential as "fertility islands". The specific objectives are: (1) to evaluate the biodiversity significance of BSCs in patches and interpatches, (2) to analyze the physical and chemical soil properties influencing soils with and without BSCs in these areas, and (3) to determine how the combination of these soil properties affects BSC presence, patch and interpatch conditions, and their interaction. By improving our understanding of BSC ecology and its role in ecosystem dynamics, the findings of this study can offer valuable insights into promoting sustainability in arid environments.

2. Materials and Methods

2.1. Study Area

BSC sampling was carried out at two sites located in arid ecosystems of central-western Argentina, characterized by similar lithologies, distributions, and types of BSCs, "El piedemonte" in the province of Mendoza and "Pedernal" in the province of San Juan, Argentina.

These sites were selected to represent the ecological variability within the arid ecosystems of central-western Argentina. Although 'El Piedemonte' and 'Pedernal' exhibit differences in their microclimatic conditions, soil textures, and vegetation types, this study aimed to evaluate general patterns of biological soil crust presence and functionality across the region. Consequently, data from both sites were analyzed collectively to identify overarching trends rather than site-specific differences.

The piedmont is located in the district of Capdevile (32°43′24.3″ S, 68°50′29.69″ W), province of Mendoza at 741 m above sea level, in the Andean piedmont (Figure 1). The climate is continental, with an average annual rainfall of 220 mm, concentrated mainly in summer (December–February). The average annual temperature is 17.5 °C, with a maximum of 30 °C in summer and a minimum of 3 °C in winter [22,39] (pp. 101–105). The soils with a depth of approximately 5 m are classified as Entisols and Typic Torrifluvents [23,40], with a uniform sandy-loam texture throughout the profile. The surface layer includes a notable presence of fine gravel and coarse sand, contributing to an irregular distribution of biocrusts due to their limited capacity to retain water and nutrients. The area is a scrubland characterized by patches of vegetation that are usually formed by a single individual of the species *Larrea cuneifolia* Cav. [24,25,41,42] separated by interpatches with very abundant physical crusts and BSC. The plants measure approximately 0.8 m in height and 1.0 m^2 in cross-section [25,42] (Figure 2). The BSCs are dominated by mosses such as *Pseudocrossidium arenicola* (Taylor) R.H. Zande (80%), *Bryum argenteum* Hedw. (67%), and *Tortula atrovirens* (Sm.) Lindb. (40%), lichens such as *Catapyrenium squamulosum* (Ach.) *Breuss* (72%), *Enchylium coccophorum* (Tuck.) Otálora, P.M. Jørg. and Wedin (93.3%), and the cyanobacteria are represented by *Scytonema tolypothrichoides* Kützing ex Born. and Flah (70%), the mean coverage value for biocrusts is 42.3% [26,43]. BSCs exhibit a heterogeneous distribution, with well-developed patches and less-developed intervening spaces (Figure 1).

Pedernal is located in the southwest of the province of San Juan (32°00′8.43″ S; 68°45′10.18″ W) at 1139 m asl, in the area called "Pedernal Protected Landscape" [27,44] (Figure 1). The average annual temperature is around 18 °C with a minimum of 6 °C and a maximum of 20.7 °C and precipitation is 370 mm [27,28,39,44,45]. The aridity index is 10.9 according to De Martonne [29,46]. The soils correspond to Entisols in the typical torrents with sandy loam texture (68% sand, 22% silt, 15% clay) [23,40]. The surface soil is rocky to gravelly in texture, with scattered gravel-sized particles that limit the establishment of biocrusts and result in their patchy distribution. The area is a scrubland characterized by vegetated patches that are usually formed by a single individual of the species *Zuccagnia punctata* Cav separated by interspaces with physical crusts and very abundant BSCs. The plants measure approximately 0.8 m in height and 1.4 m^2 in cross-section [25,42] (Figure 2). In this site, BSCs cover around 21% of the soils and are dominated by the mosses *P. arenicola* (56.6%) and *T. atrovirens* (35%), and lichens such as *E. coccophorum* (82%) and *Placidium lachneum* (Ach.) Breuss (72%) [26,43]. The BSCs exhibit an irregular distribution, with well-developed patches and less-developed interpatches.

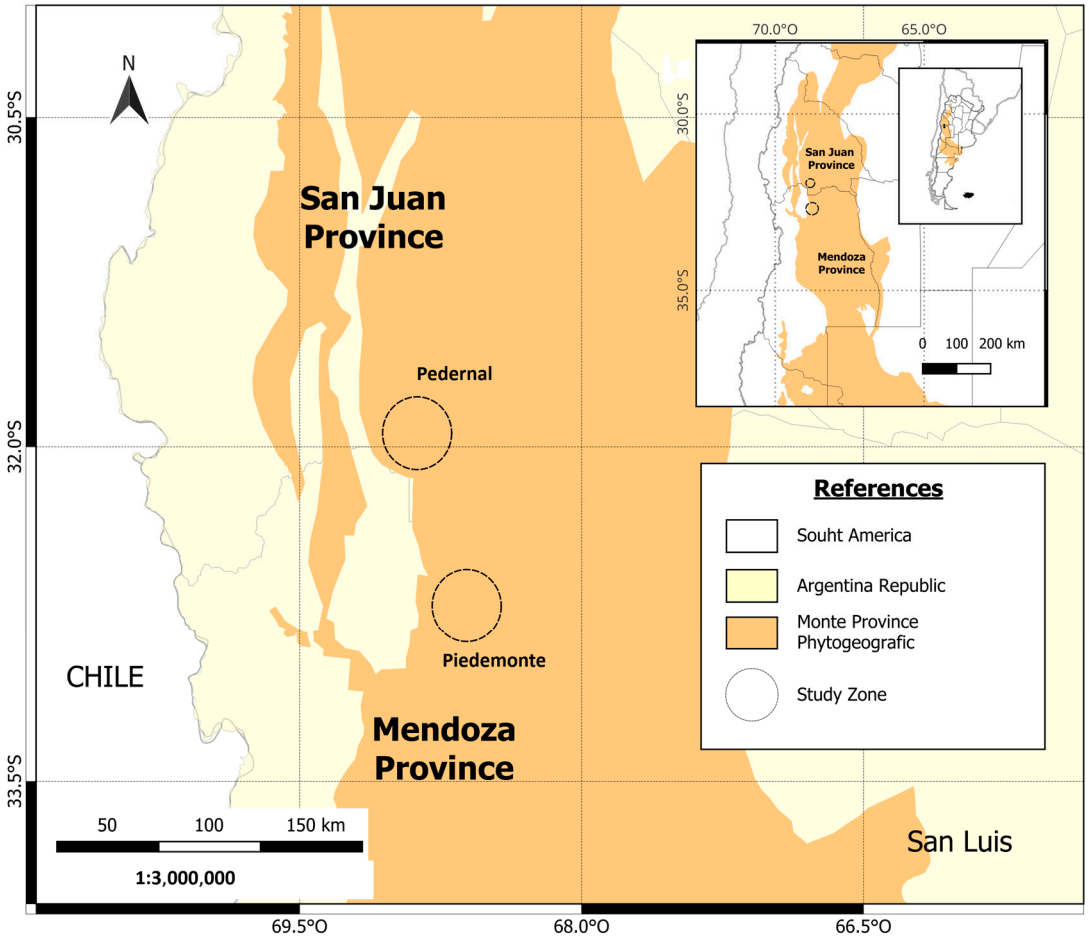


Figure 1. Map showing the study area with the location of the two analyzed sites.

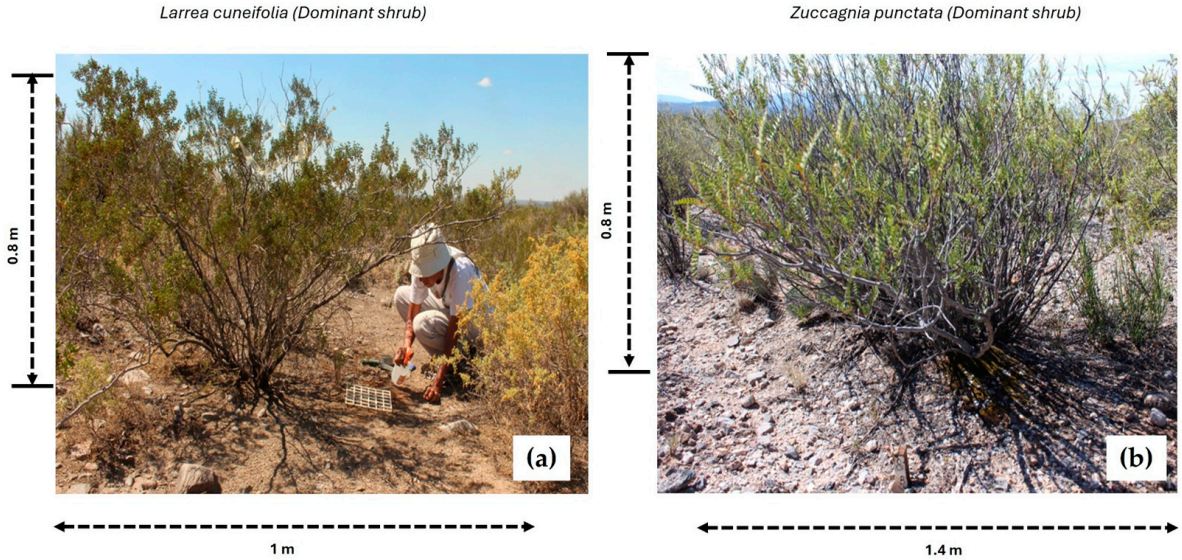


Figure 2. Photograph showing the two dominant species at each site, with their typical morphology. (**a**) *Larrea cuneifolia* in the Piedemonte region, showcasing its characteristic shrub-like structure adapted to arid environments. (**b**) *Zuccagnia punctata* in Pedernal, displaying its distinctive morphology suited to high-altitude arid zones.

2.2. Experimental Design

Sampling was carried out at the beginning of the period of maximum rainfall, in early spring, when the period of maximum activity of the BSCs occurs. The study area for each site was selected to represent typical conditions of the ecosystem, minimizing anthropogenic disturbances and ensuring accessibility. First, the proportion of vegetation patches and interpatches occupied by BSCs we quantified using the modified point quadrat method by Passera et al. [30,47]. For this purpose, 10 linear transects were made, per study site, of 10 m length. The first transect was placed randomly within this representative area to avoid bias in the initial sampling location. Subsequent transects were systematically located at a distance of 10 m from the first. In each transect, the presence or absence of aerial vegetation and BSCs every 10 cm were recorded (total of points per transect equals 100) was used to determine the functional group coverage of BSCs and vascular plants [31,48].

Secondly, to evaluate the functionality of BSCs in patches and interpatches, a total of 60 plots were made at each sampling site. For this purpose, 30 areas were randomly selected in soils located under the center of the canopy of the dominant shrub (called patch) and 30 areas in intermediate open spaces (called interpatches) at each study site. We took advantage of the heterogeneity in the distribution of BSCs in the patch and interpatch to select the subzones with BSCs and without BSCs (see Figure 3).

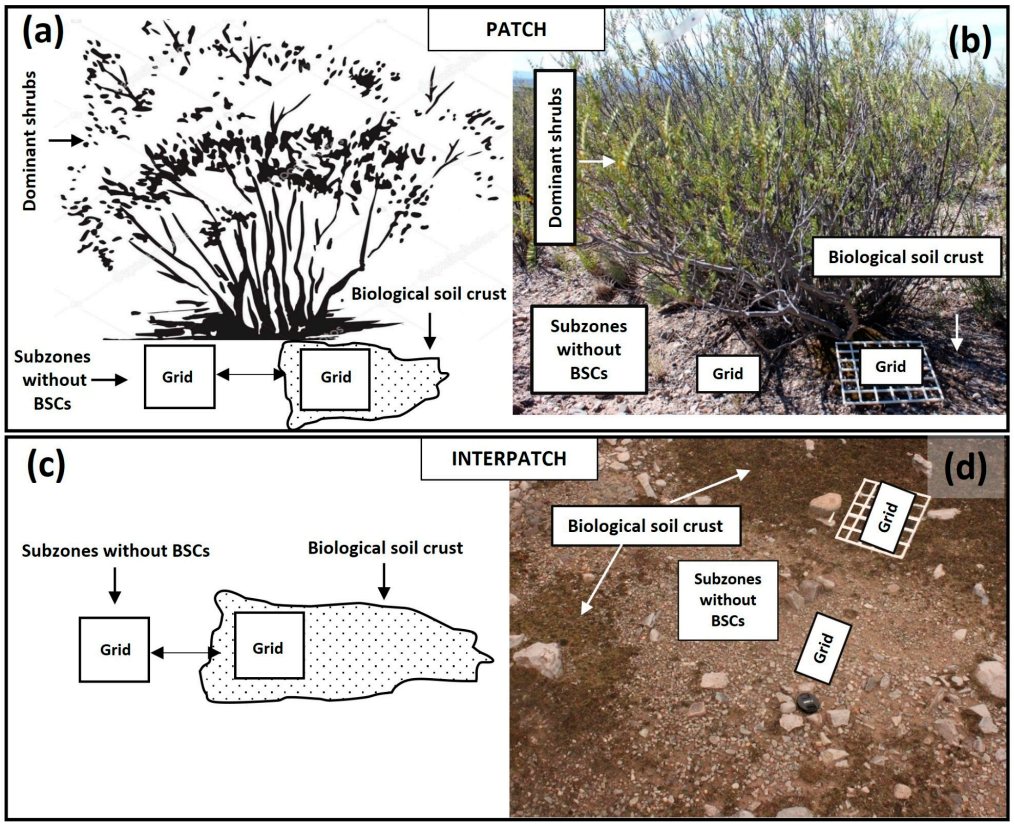


Figure 3. Schematic representation and field images illustrating the sampling methodology for biological soil crust (BSC) functionality assessments in patches and interpatches. (**a**) Diagram of a vegetation patch, showing two subzones: areas without visible BSCs and WBSC areas with visible BSCs. (**b**) Field photograph showing a vegetation patch and the sampling grid used to record BSC species distribution. (**c**) Diagram of an interpatch area, similarly, divided into subzones. (**d**) Field photograph of an interpatch area with the sampling grid.

A square plastic grid measuring 24.5 cm in length was installed within each subzone. In each subzone, leaf litter was removed, and the soil was moistened with a spray to achieve greater visibility of the mosses before placing the plastic grid on the soil surface. Each grid contained a total of 36 cells, each 3.5 cm long per side and 0.5 cm thick. The absolute

frequency of each BSC species was recorded in each grid square. Subsequently, an intact soil core was extracted from below each grid by inserting an aluminum tube into the soil to a depth of 3 cm to analyze the soil properties. Samples in the without BSC subzones were collected similarly after removing leaf litter. The superficial soil layer (0–3 cm) was selected for analysis as it represents the zone where biological soil crusts (BSCs) exert their greatest influence on soil properties, as demonstrated in numerous studies [49–51]. BSCs primarily affect the upper 1–5 cm of the soil, driving key processes such as nitrogen fixation, organic matter deposition, moisture retention, and soil aggregate stabilization [14,23]. These effects are particularly critical in arid ecosystems, where the role of BSCs in maintaining soil functionality is most pronounced. The 0–3 cm depth also aligns with established protocols in BSC research, such as those by Herrick et al. [52], which recommend sampling the layers most impacted by biocrust activity. Sampling at this depth minimizes dilution effects caused by deeper soil layers, which are less affected by the processes regulated by BSCs, ensuring a clear evaluation of BSC-driven processes and allowing for comparability across similar studies [23,49].

2.3. Taxonomic Identification

Identification of BSCs was initially carried out in situ, based on their morphological and anatomical characteristics, following Eldridge and Rosentreter [53]. Species were identified to genus and species level when possible. To corroborate the identification, the material was collected and transported to the laboratory. The presence of lichens and mosses was determined by direct and microscopic observation, using morphological features. The specimens were air-dried in paper bags and stored for further identification in two public herbaria: the Ruiz Leal Herbarium (MERL), which belongs to the Argentine Institute for Research in Arid Zones (IADIZA-CONICET), and the Herbarium of the Museum of Natural Sciences of the Province of San Juan, which belongs to the National University of San Juan. The collected BSC samples were hydrated for 24 h in the laboratory for the identification of bryophytes. Observation of morphological characteristics was carried out with a dissecting microscope with an integrated scale and the anatomical features were examined under a compound optical microscope after placing the samples in water. To observe the cellular characteristics, the stem and leaves of the mosses were cut transversely by hand. The lichen species were determined by morphological, anatomical, and chemotaxonomic analysis, using a magnifying glass to examine their morphological characteristics. For the chemotaxonomic analysis, several chemical staining reactions were performed. The chemical reactions were performed with 10% potassium hydroxide (KOH), sodium hypochlorite at commercial concentration (NaClO), K (potassium) before C (carbon) (KC), iodine solution of 0.5% to 1.5% iodine in 10% IK (Lugol's), and aqueous solution for 50% nitric acid. To identify the cyanobacterial species, cultures were performed in the laboratory using the technique developed by Watanabe [54], under controlled conditions of temperature (20–30 °C) and photoperiod (12 h of light - 12 h of darkness) for 30 days. Observations were made with an optical microscope (OLYMPUS BX50). The size of vegetative cells, sheaths, filaments, and trichomes was measured, and the presence and position of specialized structures were determined. In addition, morphological characteristics such as aggregation pattern, composition, presence of mucilage, shape, color, and size of cells were analyzed. Photographs were taken with a CANON T5 camera (18 megapixels). Cyanobacteria identification was performed following taxonomic keys [55–59]. Lichens were taxonomically determined following Brodo [60], and Nash [61], and bryophyte determination was performed following Flowers [62], Brummitt and Powell [63], and Sharp [64].

2.4. Analysis of the Physicochemical Properties of Soil Crusts

In each patch and interpatch the following physical properties were determined: aggregate stability (ST), compaction (CO), temperature (T°), and moisture (M). To evaluate the stability of the aggregates, 16 subsamples of soil with an approximate diameter of 6–8 mm were randomly collected in each patch and the stability was measured in each

one using the test described by Herrick et al. [52]. The compaction was measured with a geotester punctual penetrometer (Brand: Part # 59035 Geotester Penetrometer) and according to the particle size of the soil, the standard was modified following Bucchi [65]. Three measurements were made per replicate. To determine the influence of the BSCs on the temperature, the temperature values were recorded at −1 cm from the ground level. A bimetallic thermometer was used for the record. The measurements were punctual and were made at fixed times between 12:00 and 13:30 h in situ. Moisture was assessed using the gravimetric method, drying the samples in an oven at 105 °C for 24 h.

For determination of chemical properties: Soil samples collected from patch and interpatch were air dried and manually sieved through a 2 mm sieve before laboratory analysis to acquire the fine soil fraction. During sieving, roots and other debris were removed. Each sample was analyzed for the following chemical properties: total nitrogen (N), phosphorus (P), and organic matter (OM). Total nitrogen was assessed by Kjeldahl acid digestion with $SeSO_4$ eK_2SO_4 as a catalyst in a Tecator 20 digestion system [66]. For phosphorus determination, soil samples were extracted with 0.5 M sodium bicarbonate ($NaHCO_3$) at pH 8.5 following the method reported by Murphy and Riley [67]. The extract was then analyzed using flame photometry. OM was determined by the loss on ignition technique [68] and performed on a Kjeltecauto 1030 analyzer (Tecator, Sweden). Likewise, the following physicochemical properties were determined: electrical conductivity (EC) and hydrogenation potential (pH). EC and pH were measured in a 1:1 soil-water suspension [69] using an EC meter (Hach Sension 5) and a pH electrode (Orion research digital ionalyser/501), respectively.

2.5. Data Analysis

Abundance was determined as the number of cells per grid in which the species was detected. Species richness was determined as the number of species per microsite (patch-interpatch). The relative frequency of each species was also calculated as the number of times each species appeared in the total number of grids sampled.

$$FRi = Pi \times NS, \quad (1)$$

where FRi is the relative frequency of species i concerning the total frequency, Pi is the number of grids in which species i was present, and NS is the total number of sampling grids.

Species diversity was estimated using the Simpson index (H').

$$H' = 1 - \sum(ni\ (ni - 1)N(N - 1)), \quad (2)$$

where N is the total number of individuals of all species detected and ni is the number of individuals of species i. The Simpson index produces values between 0 and 1; values close to 1 indicate greater dominance of a species, while values close to 0 reflect greater diversity in the habitat.

The similarity in species composition between microsites was determined by the proportional similarity index (PS), calculated as:

$$PS = 1 - 12\sum |\, pi_A - pi_B \,|, \quad (3)$$

where pi_A and pi_B are the relative proportions of species i at sites A and B, respectively. PS values range from 0 (no common species) to 1 (identical composition and proportions).

For the second objective, ANOVA models were performed taking into account the physicochemical properties of the soil, the patches and interpatches, and the relative abundance by species within each plot. Normality was verified using the Kolmogorov—Smirnov test and homoscedasticity with the Levenne test. The analyses were performed considering an $\alpha \leq 0.05$. In addition, a linear discriminant analysis, LDA, was performed.

In the third objective, we applied a multivariate analysis of variance (MANOVA) to evaluate the simultaneous effects of soil physicochemical properties on the presence or absence of BSCs, patch and interpatch conditions, and their interaction. Multivariate contrasts were monitored using univariate contrast analysis. To track these contrasts, we

performed a post hoc analysis with a Bonferroni adjustment. If the data were not normally distributed, a Kruskal–Wallis test with pairwise comparison was performed. All statistical analysis was performed using RStudio software (version 2024.09).

3. Results

The results presented in this study reflect an integrated analysis of data from 'El Piedemonte' and 'Pedernal', focusing on general patterns of BSC functionality and soil physicochemical properties across the central-western Argentine arid landscape. While the two regions exhibit environmental variability, the joint analysis allows for a broader understanding of BSC dynamics under diverse conditions, capturing the overall role of these communities in arid ecosystems.

3.1. Biodiversity of BSCs in Patches and Interpatches

Vegetation covers approximately 45.5% of the total area at the study sites, with the remainder of the area being interpatch spaces, including litter, and rock. BSCs covered 45.8 ± 3.5 and 44.3 ± 3.8% of the area under shrub canopies (patches) and in interpatches, respectively (Table 1). BSCs in vegetation patches and interpatches are similar in total cover, species richness, and diversity (Table 1). BSCs composition varied by location; soils with BSCs under vegetation patches are dominated by mosses, while soils with BSCs under vegetation patches are dominated by cyanobacteria and lichens. These differences in specific composition reflect how BSCs adapt to the microenvironmental conditions of their respective microsites (Figures 4 and 5). Of the total number of grids evaluated, in the patch condition, 44.4% were dominated by mosses, 19.8% by cyanobacteria, and 30.2% by lichens while in the interpatch condition 58.6% by cyanobacteria, 40.5% by lichens, and 0.9% by mosses (Table 1, Figure 4). In terms of diversity and species richness, patches showed a higher total number of species compared to interpatches. The families Verrucariaceae (lichens), Pottiaceae (mosses), and Oscillatoriaceae (cyanobacteria) presented the highest species richness. Simpsons' diversity index (H) showed higher diversity in patches (H = 0.08) than in interpatches (H = 0.11), suggesting that vegetation cover contributes to a higher biological diversity of BSCs. The similarity index (SP) revealed that patch and interpatch shared quite a few species in common (SP = 0.6).

Table 1. Mean percentage cover, standard deviation (SE), and relative abundance by species of mosses, lichens, and cyanobacteria for soils in vegetation patches and interpatches.

Specie	Patch	Interpatch
Moss	44.4	21.38
Aloina catillum (Müll. Hal.) Broth.	0.1 (0.05)	—
Bryum argenteum Hedw.	6.2 (1.2)	5.5 (1.5)
Bryum lanatum (P. Beauv) Brid	1.6 (0.2)	1.0 (0.5)
Bryum sp.	4.6 (0.5)	11.0 (2.5)
Pseudocrossidium aff. replicatum	4.2 (0.5)	—
Pseudocrossidium arenicola (Dusen) M.J. Cano	12.4 (2.6)	1.1 (0.5)
Pseudocrossidium chilensis R. S. Williams	2.5 (0.3)	0.2 (0.1)
Pseudocrossidium obtusulum (Lindb) H.A. Crum and L.E. Anderson	2.9 (0.3)	0.2 (0.1)
Pseudocrossidium replicatum (Taylor) R.H. Zander	0.8 (0.1)	—
Pseudocrossidium sp.	1.7 (0.5)	0.0
Pterygoneurum ovatum (Hedw) Dixon	0.7 (0.2)	0.5 (0.1)
Pterygoneurum subsessile (Brid) Jur	0.1 (0.05)	0.1 (0.05)
Tortula atrovirens (Sm.) Lindb	6.2 (2.5)	1.7 (0.1)
Riccia sp.	0.2 (0.05)	0.1 (0.05)

Table 1. *Cont.*

Specie	Patch	Interpatch
Lichens	43.4	46.9
Buellia elegans Poelt	0.6 (0.1)	—
Clavascidium lacinulatum (Ach) M. Prieto	6.7 (2.4)	5.5 (2.1)
Diplochistes diacapsis (Ach)	0.5 (0.1)	—
Enchylium coccophorum (Tuck)Otálora, P.M. Jørg. and Wedin	21.3 (3.9)	25.3 (6.9)
Enchylium tenax (Sw.) Gray	2.4 (0.5)	3.0 (1)
Heppia sp.	0.8 (0.4)	1.0 (0.5)
Placidium lachneum (Ach.) Breuss	5.1 (1.8)	9.0 (3.8)
Placidium squamulosum (Ach.) Lumbiocrusth	1.2 (0.5)	1.5 (0.6)
Psora decipiens (Hedwig) Hoffm	3.0 (1)	1.5 (0.7)
Psora tuckermanii R. A. Anderson	1.2 (0.9)	0.2 (0.1)
Toninia sedifolia (Scop) Timdal	0.6 (0.1)	—
Toninia tristis (Th. Fr.) Th.Fr.	0.1 (0.05)	—
Peltula obscurans	0.7 (0.1)	0.8 (0.4)
Cyanobacteria	11.6	30.8
Lynbya sp.	0.1 (0.05)	0.4 (0.2)
Microcoleus vaginatus (Voucher) Gomont	0.4 (0.1)	0.4 (0.1)
Nostoc calcicola Brébisson ex Born. et Flah	0.2 (0.1)	0.3 (0.1)
Nostoc entophylum Born. et Flah	0.2 (0.1)	0.4 (0.2)
Nostoc muscorum Ag. ex Born. et Flah	0.1 (0.05)	0.5 (0.2)
Nostoc paludosum Kützing ex Born. et Flah	0.2 (0.1)	0.3 (0.1)
Nostoc sp.	0.2 (0.1)	0.1 (0.05)
Oscillatoria obscura Bruhl et Biswas	0.3 (0.1)	1.4 (0.8)
Oscillatoria sp.	0.3 (0.1)	1.3 (0.9)
Oscillatoria subbrevis Schmidle	0.1 (0.05)	—
Phormidium angustissimum W et. G. S. West	0.6 (0.3)	4.0 (2.1)
Phormidium fragile (Meneghini) Gomont	0.8 (0.5)	6.0 (2.8)
Phormidium rubroterricola Gardner	0.3 (0.1)	2.1 (1.1)
Scytonema millei Bornet ex Born. et Flah	0.4 (0.2)	0.7 (0.5)
Scytonema tolypothricoides Kützing ex Born. et Flah	7.5 (2.5)	12.5 (3.1)
Anabaena anomala Fritsch	—	0.2 (0.1)
Nostoc punctiforme (Kütz) Hariot	—	0.3 (0.1)

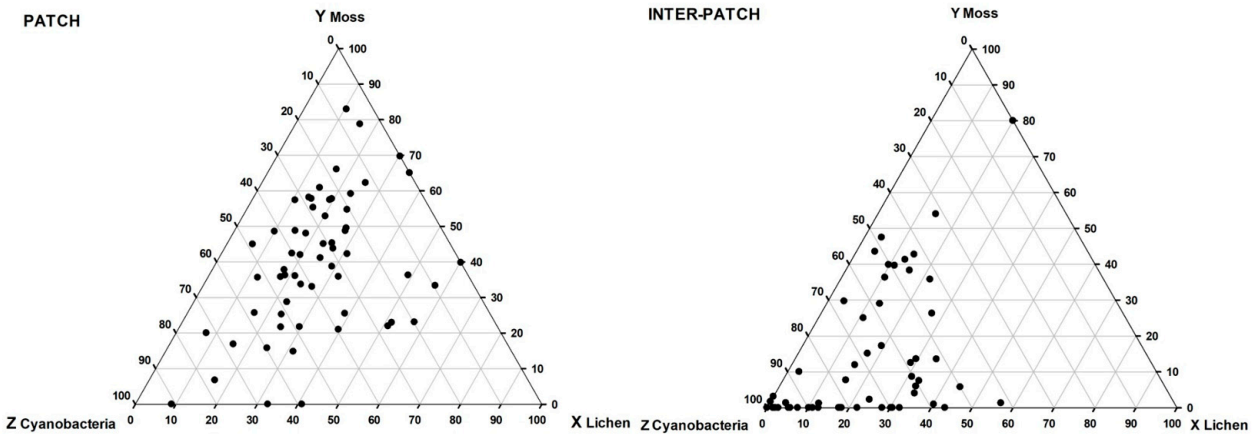


Figure 4. Coverage of a functional group of BSC (cyanobacteria, moss, and lichen) on patch and interpatch. Each point in the ternary plots represents an individual sample, showing the relative coverage of the three functional groups in the sampled microhabitat. The left plot corresponds to samples taken in patches, and the right plot corresponds to samples taken in interpatches.

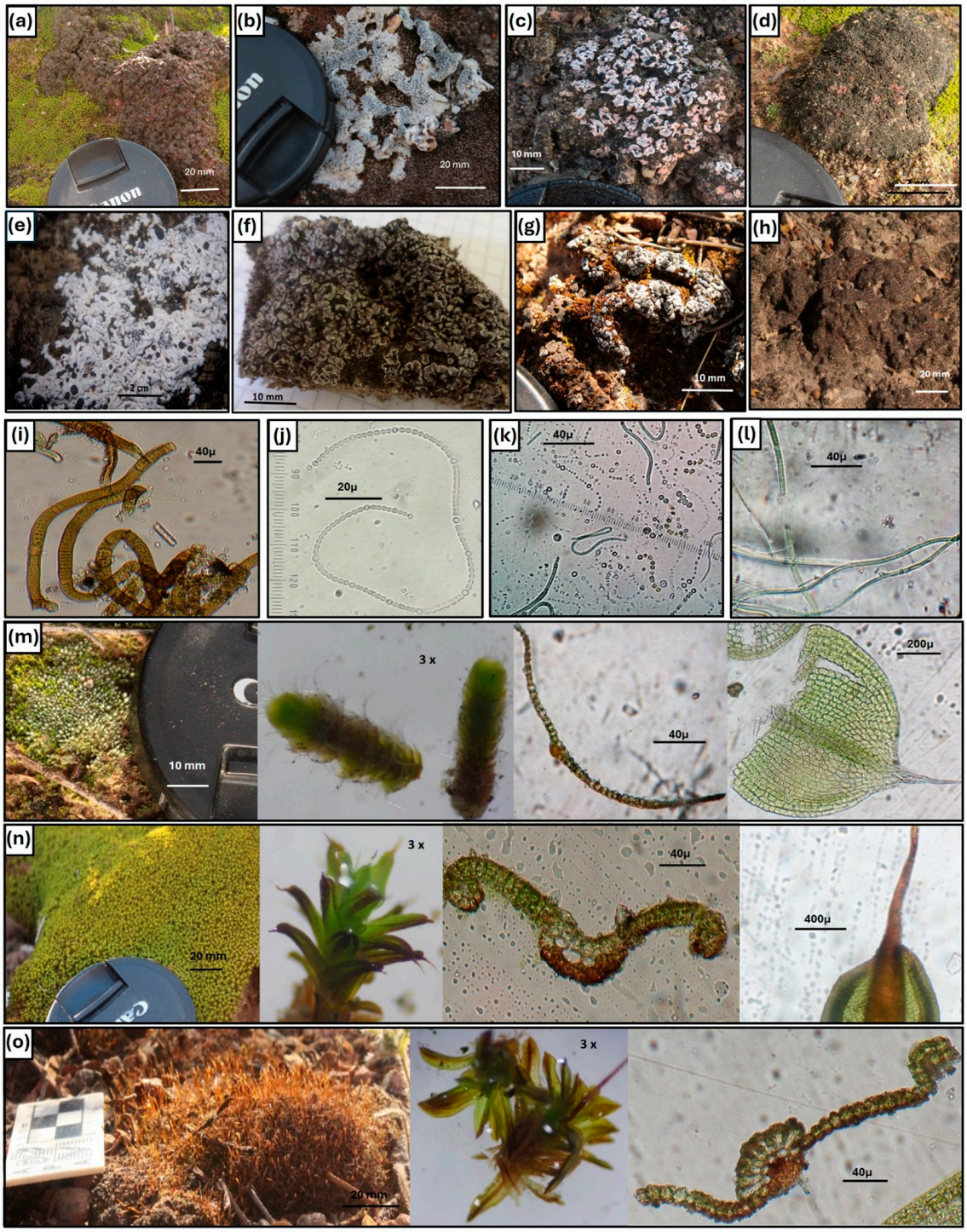


Figure 5. Micro-photographs of most frequent components of biocrusts found. Species of lichens: (**a**) *Placidium squamulosum* (**b**) *Diplochistes diacapsis*, (**c**) *Psora decipiens*, (**d**) *Enchylium coccophorum* (**e**) *Buellia elegans* (**f**) *Psora tuckermanii* (**g**) *Toninia sedifolia* (**h**) *Placidium lachneum*. Species of cyanobacteria: (**i**) *Scytonema* sp., (**j**) *Nostoc* sp., (**k**) *Phormidium* sp. (**l**) *Oscillatoria* sp. Species of briophytas: (**m**) *Bryum* sp. (**n**) *Pseudocrossidium arenicola* (**o**) *Tortula atrovirens*.

3.2. Effect of BSC on Soil Properties

The principal component analysis determined that canonical axis 1 explained 78.1% of the variation between groups, while axis 2 explained 20.9% of the variability. For canonical axis 1, the most important variables were organic matter (OM), electrical conductivity (EC), compaction (CO), and phosphorus (P). While the most important variables for dis-

crimination in canonical axis 2 were soil stability (ST), nitrogen (N), moisture (M), and temperature (T°) (Figure 6). Compaction, organic matter, and phosphorus were able to discriminate between patches without BSC. Likewise, temperature was able to discriminate the interpatch groups with and without BSC. Finally, soil moisture, stability, and nitrogen concentrations discriminated between patches with BSC. The overall classification error rate was 25%, highlighting the complexity and variability of BSC effects.

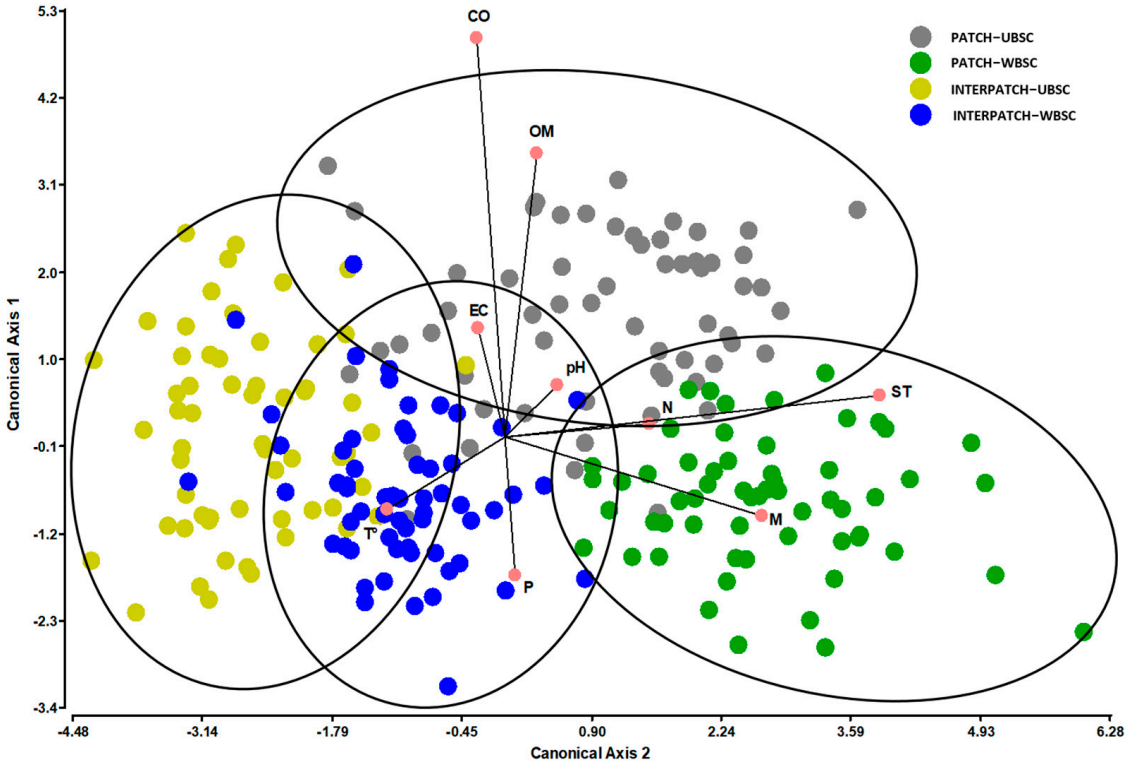


Figure 6. Relationship between types of microsites and their influence on variables with discriminatory potential through a multivariate statistical procedure, such as line discriminant analysis (LDA). CO (Compaction), OM (Organic matter), EC (electrical conductivity), T° (Temperature), P (phosphorous), N (nitrogen), M (moisture), ST (stability), pH. Patch−UBSC and patch−WBSC (patches without and with BSC, respectively). Interpatch−UBSC and interpatch−WBSC (interpatch without and with BSCs, respectively).

At patch and interpatch sites, BSCs significantly increased stability, moisture, and total nitrogen and phosphorus levels. In addition, BSC decreased compaction which increases soil porosity, temperature, and electrical conductivity (EC). No significant changes were observed in pH (Figure 7). As for OM% concentrations, the interpatches without BSC showed significant differences from the rest (Figure 7).

Soil stability values were significantly higher in patches than in interpatches (Figure 7). Within patches, areas with BSC (WBSC) showed higher stability compared to areas without BSC (UBSC) (Figure 7). A similar behavior was observed within interpatches: WBSC areas showed higher soil stability values (Figure 7). Soil compaction was significantly lower in the subzones with BSC, both in patches and interpatches (Figure 7). Subzones WBSC had significantly lower temperatures compared to subzones UBSC, both in patches and interpatches. WBSCs maintained significantly higher moisture levels than UBSC subzones, both in patch and interpatches. BSC had a significant effect on most soil chemical properties. N and P levels were higher in WBSC areas both in patches and interpatches (Figure 7). BSCs had a significant effect on most soil physicochemical properties. In particular, EC levels were higher in areas without UBSCs at both subzones (Figure 7). The pH did not show significant differences between interpatch patches.

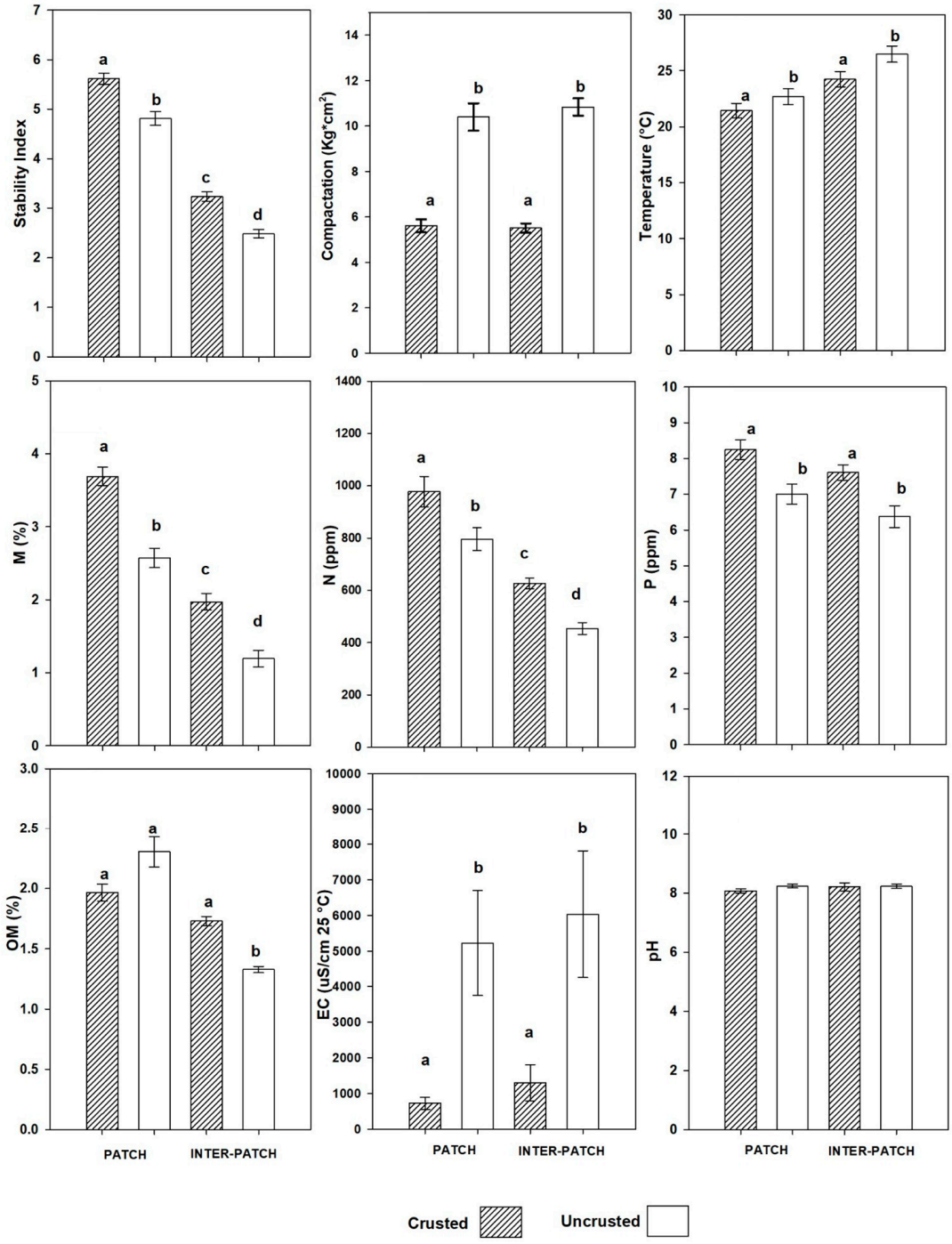


Figure 7. Mean values and standard deviation of stability, compaction (kg cm^2), nitrogen concentrations (ppm), phosphorus concentrations (ppm), organic matter (%), electrical conductivity EC (µS/cm 25 °C), moisture (M), temperature and pH, for the areas with biocrust (WBSC) vs. the area without biocrust (UBSC) in patches (**left**) and interpatch (**right**) for the study sites. Different letters indicate significant differences ($\alpha \leq 0.05$).

3.3. Effect of BSC Presence in Patches and Interpatches and Their Interaction

The presence of BSC at the soil surface had a significant multivariate main effect on soil physicochemical properties. Although the microsite (patch vs. interpatch) also affected some properties such as stability, moisture, and organic matter, the impact of BSC presence affected more soil properties (Table 2). Since the presence of BSC affected the properties of

compaction, stability, temperature, moisture, and total phosphorus, the interaction between the microsite and the presence of BSC only influenced pH (Table 2).

Table 2. Results from MANOVAs testing the effects of microsite (patch and interpatches) and BSC (presence/absence) on soil.

	Microsite		BSC		Interaction	
	F	***p*-Value**	**F**	***p*-Value**	**F**	***p*-Value**
Compaction (Kg × cm^2)	1.50	0.20	9.10	0.00 *	1.10	0.20
Stability	93.80	0.00 *	6.90	0.01 *	3.00	0.09
Temperature (°C)	1.40	0.20	10.40	0.00 *	0.20	0.60
Moisture (%)	6.00	0.00 *	11.00	0.00 *	0.00	0.94
Total N (ppm)	4.10	0.50	0.06	0.87	0.23	0.63
Total P (ppm)	1.08	0.30	5.60	0.02 *	0.01	0.93
OM (%)	14.30	0.00 *	1.10	0.30	5.40	0.20
EC (uS/cm 25 °C)	0.16	0.70	0.89	0.35	0.03	0.90
pH	2.00	0.17	2.80	0.10	5.40	0.03 *

* *p*-values below 0.05 are in bold (n = 60).

4. Discussion

The results of this study showed similar soil biocrust (BSC) coverage in patches and interpatches, although with differences in composition: mosses dominated in patches, while cyanobacteria and lichens were more prevalent in interpatches. Furthermore, BSC significantly influenced soil properties, underlining the importance of their location and associated vegetation in their ecological role. It also highlights the need to promote the sustainability of arid soil ecosystems, which depend on management practices that preserve biodiversity and soil health. Finally, BSC notably affected soil stability, moisture, nitrogen and phosphorus levels, and compaction, with variations depending on the microenvironment. The levels of biological soil crust (BSC) coverage observed in this study are consistent with those reported by Navas et al. [43], and Garibotti et al. [37], in similar systems, highlighting the remarkable ability of these communities to adapt to a wide range of thermal variations. These variations include fluctuations that can range from 30 to 45 °C in summer and drop below freezing in winter. This suggests that both microsites offer suitable conditions for BSC establishment, albeit with differences in species composition (Table 1, Figure 4). This similarity in total BSC cover between the two microsites indicates that both patches and interpatches provide enabling environments but favor different biocrust components.

When analyzing the species composition of BSCs, a clear differentiation between the microsites is observed (Table 1, Figure 4). Vegetation patches hosted greater diversity, with mosses dominating with 44.4% coverage. This predominance can be explained by the more stable microenvironmental conditions under the patches, where moderate temperatures and greater moisture retention create a favorable environment for mosses, which require more constant moisture levels and are more tolerant to shade [70]. In contrast, in the interpatches, cyanobacteria and lichens showed higher coverage (58.6% and 40.5%, respectively). This finding reflects their adaptation to more extreme conditions, such as greater thermal fluctuations and direct exposure to solar radiation, which are typical characteristics of these microsites [71]. The differential distribution of mosses and cyanobacteria in patches and interpatches highlights how variations in microenvironmental conditions influence the structure of BSC communities. Vegetation patches act as modulators of soil properties, altering factors such as moisture and temperature, thereby creating specific microhabitats that allow for the colonization of a greater diversity of species [43]. On the other hand, interpatches, with their greater exposure and homogeneity, select species better adapted to stress conditions, such as cyanobacteria, which can withstand desiccation and recover quickly after rehydration [72].

The greater presence of cyanobacteria and lichens in the interpatches could be related to their ability to survive in less-structured and low-fertility soils [73,74]. Lichens such as

Enchylium coccophorum, *Clavascidium lacinulatum*, and *Placidium lachneum*, dominant in our study, have also been reported in similar arid and semi-arid conditions in the Mexican Altiplano and the Monte desert in Argentina [25,43,75–77]. Their photoprotective strategies enable them to withstand high irradiation and drought, thriving in extreme environments [78].

Therefore, the health of BSCs not only promotes biodiversity but also improves the resilience of these ecosystems to climate change and human activities. Promoting the conservation of these communities is essential to ensure the sustainability of arid and semi-arid ecosystems, where each component plays a vital role in the functioning of the environment. The greater species richness and diversity observed in patches, according to the Simpson diversity index (H = 0.08 in patches vs. H = 0.11 in interpatches), highlights the role of vegetation in promoting BSC biodiversity. Vegetation patches likely provide more heterogeneous microhabitats, offering niches for a wider range of BSC species [43]. The high similarity index (SP = 0.6) between patches and interpatches suggests significant species overlap, but also that each microsite harbors a unique subset of the BSC community, thereby contributing to landscape-scale diversity [79,80]. As mentioned above, these results have important ecological implications, especially in the context of the stability and resilience of arid ecosystems. BSC dominated by mosses in patches enhances soil stability and water retention, facilitating the establishment of vascular plants and contributing to the overall resilience of the ecosystem [81,82]. On the other hand, the predominance of cyanobacteria and lichens in interpatches likely plays a crucial role in nutrient cycling and primary productivity, particularly in areas where conditions are too severe for the establishment of vascular plants [83,84].

Principal component analysis showed that canonical axis 1 explained 78.1% of the variation between groups, with organic matter, compaction, electrical conductivity, and phosphorus standing out as key variables. Canonical axis 2, which explained 20.9% of the variability, focused on soil stability, nitrogen, moisture, and temperature. Compaction, organic matter, and phosphorus were discriminated between patches without BSC, temperature between patches with and without BSC, and moisture, stability, and nitrogen between patches with BSC. These results suggest that the spatial distribution and specific composition of BSCs should be carefully considered in future studies as their effects are specific to their location, composition, and soil and environmental conditions.

In both patches and interpatches, BSCs played a significant role in enhancing soil stability and reducing compaction, though the effects varied depending on the microsite. In interpatches, areas with BSC showed higher stability compared to areas without BSC (see Figure 7). However, in the patches, an opposite trend was observed, as areas without BSC showed higher soil stability values (Figure 4). This suggests that the role of BSCs in soil stabilization may depend on both their location and the type of vegetation present. The stability provided by BSCs resulting from mechanical processes, such as fungal hyphae and cyanobacterial filaments forming a binding network, and chemical processes, such as the secretion of the mucilaginous sheath that cements particles into aggregates, thus promoting particle-to-particle adhesion [85–88]. Differences between microsites may also reflect the ability of vegetation patches to generate greater cohesion through their establishment and the addition of particles by their roots. This effect can mask or reduce the influence of BSCs on stability compared to the impact exerted by vegetation. In addition, the improvement in soil resistance thanks to the presence of BSCs not only reduces wind erosion but also water erosion, decreasing thus the vulnerability of desert ecosystems [86,87]. Furthermore, soil compaction was significantly lower in the sub-zones with BSC, both in patches and interpatches (see Figure 7). Variations in organic matter and moisture influenced susceptibility to compaction, which alters soil structure and hydrology by increasing bulk density, degrading aggregates, reducing porosity, and decreasing infiltration levels. These changes negatively affect vegetation regeneration by inhibiting seed germination and seedling growth, potentially inducing vegetation mortality [88]. The presence of BSCs mitigates these adverse effects by maintaining lower compaction, improving soil structure, and reducing both wind and water erosion. This dual role of BSCs in stabilizing soil and decreasing

compaction underscores their importance in promoting the sustainability and resilience of desert ecosystems.

The subzones with BSCs had significantly lower temperatures compared to the subzones without BSC, both in patches and interpatches (see Figure 7). The organic layer of BSC acts as a thermal barrier, preventing temperatures from reaching extreme values and reducing the impact of sudden changes. Additionally, BSC areas retain more water for longer and have higher humidity, compared to soil without BSC, which increases thermal inertia and stabilizes soil temperatures. The presence of liquid water in BSC also contributes to this buffering effect, due to the specific heat capacity of water, which helps maintain stable soil temperatures [89]. This thermal buffering could increase microbial activity and nutrient mineralization, improving nutrient flow in the soil [90] which can positively influence seed germination, plant growth, and nutrient uptake rates [91,92]. Furthermore, BSCs maintained significantly higher moisture levels than areas without BSCs, both within and between patches (Figure 7). This increased moisture retention can be attributed to the ability of BSCs to absorb large volumes of water, up to ten times or more of their weight [93]. In hot deserts, where evaporation is rapid due to high temperatures, the increased moisture in soils with BSCs has important ecological implications for sustainability. It promotes microbial activity, enhances decomposition processes and nutrient flow, and facilitates seed germination. These combined effects support plant growth and biodiversity, improve soil structure, and increase resilience against climate variability, making BSCs vital for maintaining the sustainability of desert ecosystems.

N and P levels were higher in areas with BSC both in patches and between patches (Figure 7). This increase in nitrogen is largely due to the ability of cyanobacteria and cyano lichens present in BSC to fix atmospheric nitrogen [94]. An increase in soil N of up to 200% due to the presence of BSC has been documented [95,96]. In systems where nitrogen is a limited resource, even small increases in its concentration can have a considerable impact on ecosystem functioning. In temperate deserts, between 5% and 88% of the N fixed by Nostoc has been shown to leach into the surrounding substrate [97,98]. This nitrogen can be reabsorbed by BSCs or become available in the soil, which in turn can be used by vascular plants [99]. Regarding phosphorus, although its influence has been less studied than that of nitrogen, an increase in P levels has been observed in soils with BSC, possibly due to the activity of P-releasing microfungi. This could be due to the ability of BSC to reuse essential elements and compete with vascular plants for minerals when conditions are optimal [91]. Phosphorus is crucial for plant growth, involved in key metabolic processes such as photosynthesis, energy transfer, and carbohydrate synthesis. However, P availability in soil is generally low, as most of it is in chemically stable forms. The ability of BSC to alter these levels and make P more available can have a significant impact on the ecosystem services these systems provide.

OM% concentrations showed a different behavior depending on the microsite. In patches, OM% was higher in areas without BSC, while in interpatches it was higher in areas with BSC (see Figure 7). This behavior can be explained by the capacity of BSC to fix atmospheric carbon [100] and generate organic matter through decomposition or production of extracellular polysaccharides [101]. It has been reported that the polysaccharide content in dense BSC can be 1.5 to 3 times higher compared to less dense covers [102]. Carbon additions by BSC are critical, as increases in carbon content stimulate microbial activity, accelerate plant matter decomposition, and increase nutrient availability to plants.

BSCs had a significant effect on most soil physicochemical properties, particularly EC and pH. EC levels were higher in areas without BSCs at both microsites (see Figure 7), likely because soils without BSCs tend to be micro-topographically lower, favoring water accumulation and subsequent evaporation, which leaves substantial amounts of salt on the surface [38,103]. Organic matter (OM) may also contribute indirectly to these differences, as its influence on water retention and soil structure could modulate evaporation rates and salt deposition. Over time, salinity in these areas could accumulate to very high levels, aggravated by increased infiltration in some types of BSCs, which would further increase

EC levels. In contrast, pH remained relatively stable between areas with and without BSCs, though soils under BSCs presented slightly lower pH values compared to bare soils (Figure 7). This aligns with the findings of Perez [104], who observed a pH reduction of 0.13 to 0.54 units under biocrusts. reported by. Lower pH levels can be beneficial by increasing the availability of certain nutrients and reducing the rate of processes like carbonate formation, which may improve soil fertility [1,105]. However, biocrust functions such as nitrogen fixation are also pH-dependent, with optimal rates typically at pH 7 or above, reduced rates between pH 8 and 10, and an increase in fixation between pH 4 and 8. These findings suggest that while the impact of BSCs on pH-related processes is mild at these sites, their influence on EC and nutrient availability highlights their importance in shaping soil properties and ecosystem functions.

The observed differences in soil properties between patches and interpatches underline the importance of BSCs in creating spatial heterogeneity in dryland soils. This heterogeneity can influence plant distribution and dynamics, as well as the structure and function of soil microbial communities. It is important to note that the role of BSCs in enhancing soil stability, water retention, and nutrient availability underscores their critical importance for promoting the sustainability of arid ecosystems. These crusts contribute to soil health by reducing erosion, maintaining soil structure, and improving moisture retention—factors that are vital for supporting vegetation growth in harsh conditions. In the context of climate change and increasing desertification, the conservation and management of BSCs become even more essential. Sustainable land management practices that protect and restore BSCs can help maintain biodiversity, promote ecosystem resilience, and enhance the capacity of arid environments to adapt to environmental stressors. By improving soil conditions, BSCs also support sustainable agricultural practices and prevent land degradation, making them key components in efforts to mitigate the impacts of climate change in vulnerable regions.

5. Conclusions

Our results highlight the crucial role of biological soil crusts (BSCs) in soil stability, compaction, and electrical conductivity. The impact of BSCs varies depending on the microsite (patch or interpatch). Overall, BSCs contribute to increased soil stability, decreased compaction, and reduced electrical conductivity in both microsites. pH turned out to be less sensitive to the presence of BSCs.

Assessing the impact of BSCs in different microsites is essential to understanding their dynamics in each ecosystem. BSCs in interpatches, far from being infertile areas, act as fertility sites, challenging the traditional conception of these spaces as unprotected and depleted. In reality, interpatches not only offer the availability of macro and micronutrients but also favor hydrological processes, benefiting the surrounding micro-ecosystem.

The importance of BSCs in improving soil physicochemical properties underlines their role in preventing soil degradation. Their loss can be a significant cause of environmental deterioration. The modifications that BSCs produce in soil stability, compaction, pH, conductivity, and texture could be used to develop qualitative indicators of soil health in these areas.

Understanding how BSCs interact with their environment and alter soil conditions is essential to assess their influence on resource availability and overall ecosystem functioning. The changes that BSCs induce in soil physicochemical properties have significant implications for resource regulation and their availability to other ecosystem components.

The role of BSCs in promoting sustainability is evident in their ability to enhance ecosystem resilience and stability. Their influence on soil properties, such as improving stability and reducing compaction, directly contributes to the long-term health and productivity of arid landscapes. By maintaining soil integrity and reducing erosion, BSCs help prevent land degradation, a critical concern in dryland areas susceptible to desertification. Additionally, their role in nutrient cycling and water retention supports vegetation growth, making them integral to sustainable agricultural practices and ecosystem restoration efforts. As climate change intensifies the challenges faced by arid environments, protecting and

fostering BSCs becomes a vital component of sustainable land management strategies. This ensures that ecosystems can continue to provide essential services, such as carbon sequestration, biodiversity support, and water regulation, which are crucial for maintaining ecological balance and supporting human livelihoods in these fragile regions.

This study contributes to the understanding of BSCs by revealing their distinct functional roles in patches and interpatches, emphasizing how their spatial distribution and specific interactions with soil properties enhance the sustainability of arid ecosystems. These findings address critical knowledge gaps, particularly in underexplored regions like central-western Argentina, providing valuable insights for sustainable land management and ecological restoration strategies.

Author Contributions: A.L.N.R.: conceptualization, formal analysis, data curation, methodology, software, writing—original draft preparation, investigation, writing—review and editing; M.A.H.M.: conceptualization, data curation, investigation, methodology, validation, writing—original draft preparation; V.F.-M.: software, formal analysis, writing—original draft preparation, writing—review and editing; E.M.C.: conceptualization, methodology, resources, visualization, supervision, project administration, funding acquisition; G.M.: visualization, supervision, project administration; R.R.: resources, writing—review and editing, visualization, supervision, project administration, funding acquisition. All authors have read and agreed to the published version of the manuscript.

Funding: The authors wish to thank the support of the following Argentine institutions: Lafarge Holcim-CONICET Project and the Scientific and Technological Research Fund (FONCYT, PICT 2015-1455); the University of San Juan (PDTS Res. 1054/18) (CICITCA 2023–2024. Res.21/I1578); the University of Comahue (PIN 2022-04/I260); National Scientific and Technical Research Council, CONICET (Project PIP 2021–2023—No. 11220200100950CO); ANPCYT (FONCYT-PICT 2019-01810); FONCYT-PICTA RESOL-2022-87 Project Number 20 (2022). Ana Laura Navas, Viviana Fernández, Eduardo MArtinez-Carretero, Germán Mazza, and Rosa Rodriguez are Research Members of CONICET, Argentina.

Institutional Review Board Statement: Not applicable.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data will be made available on request.

Acknowledgments: We would like to thank Ricardo Mauricio for his collaboration in the fieldwork, Grupo de Geobotanica y Fitogeografia-IADIZA-CCT Mendoza, la Universidad Nacional de San Juan, CONICET.

Conflicts of Interest: The authors declare no conflicts of interest.

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