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Discovering a hidden ecological treasure: Biological soil crusts of Argentina

Sergio Velasco Ayuso[1,2,3,✉]; Edith Filippini[4]; Ana Navas Romero[5,6]; Estela Mlewski[7]; Pablo Calzada Giuntini[8]; Renato García[9] & Irene Garibotti[10]

[1] Universidad de Buenos Aires, Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales. Buenos Aires, Argentina. [2] CONICET - Universidad de Buenos Aires, Centro de Investigaciones del Mar y la Atmósfera. Buenos Aires, Argentina. [3] CNRS-IRD-CONICET-UBA, Instituto Franco Argentino para el Estudio del Clima y sus Impactos (IRL 3351 IFAECI). Buenos Aires, Argentina. [4] Centro de Ecología y Recursos Naturales Renovables Dr. Ricardo Luti, Facultad de Ciencias Exactas, Físicas y Naturales, Universidad Nacional de Córdoba. Instituto de Investigaciones Biológicas y Tecnológicas (CONICET), Universidad Nacional de Córdoba. Córdoba Argentina. [5] Instituto de Ingeniería Química, Facultad de Ingeniería, Universidad Nacional de San Juan, Grupo Vinculado al PROBIEN (CONICET-UNComa). San Juan, Argentina. [6] Grupo de Geobotánica y Fitogeografía, IADIZA-CONICET. Mendoza, Argentina. [7] Instituto Multidisciplinario de Biología Vegetal, Universidad Nacional de Córdoba (CONICET). Córdoba, Argentina. [8] Universidad de Buenos Aires, Departamento de Biodiversidad y Biología Experimental, Facultad de Ciencias Exactas y Naturales. Buenos Aires, Argentina. [9] Laboratorio de Biodiversidad y Genética Ambiental, Departamento de Ambiente y Turismo, Universidad Nacional de Avellaneda. Piñeyro, Argentina. [10] Instituto de Investigaciones en Biodiversidad y Medioambiente, Universidad Nacional del Comahue, CONICET, Bariloche, Argentina.

Abstract. Biological soil crusts (biocrusts) are topsoil, diverse communities of micro- and macro-organisms that contribute to soil stability, fertility, nutrient cycling and water dynamics in drylands. Although the number of studies on the ecology and biology of biocrusts in Argentina has increased over the last two decades, works are still scarce compared to other parts of the world. Despite the surface area occupied by drylands in our territory (~ 75 %), which also present a remarkable bioclimatic and phytogeographic diversity, biocrusts are an ecological actor that remains poorly studied. Therefore, we find it valuable to review our current understanding of biocrusts in Argentina to identify knowledge gaps and establish future priority lines of research. Here, we synthesize what we know about biocrusts in Argentina, focusing on their taxonomic composition, biological interactions within the community, distribution patterns, responses to natural and human-induced stress factors, ecosystem multifunctionality, and restoration techniques. We have identified several critical aspects of biocrust biology and ecology that should be prioritized in future works. For example, it is essential to advance taxonomic studies, incorporating molecular tools to accurately classify biocrust components, which will help us deepen our understanding of biological community interactions and allow us to improve the use of biocrusts in restoration of degraded soils. We also need to expand our understanding of how biocrusts respond to environmental factors across different spatial and temporal scales, to model their responses to future scenarios of global change. While biocrust restoration efforts are showing promising results, works are primarily focused on greenhouse or laboratory cultivation techniques, and all these efforts must be validated in the field. We consider that the diversity of Argentinean drylands offers a good natural laboratory for studying biocrusts and can serve as a model for testing hypotheses on their biology and ecology.

[Keywords: drylands, biocrusts, taxonomy, restoration, biodiversity, agriculture, grazing, fire]

Resumen. Descubriendo un tesoro ecológico escondido: Las costras biológicas del suelo en Argentina. Las costras biológicas del suelo (biocostras) son comunidades diversas de microorganismos y macroorganismos que se desarrollan en la capa más superficial del suelo en los ecosistemas áridos, contribuyendo a su estabilidad, fertilidad, ciclo de nutrientes y dinámica hídrica. Aunque en las últimas dos décadas ha aumentado el número de estudios sobre la ecología y biología de las biocostras en Argentina, estos trabajos siguen siendo escasos en comparación con otras regiones del mundo. A pesar de que los ecosistemas áridos cubren aproximadamente un 75 % del territorio argentino y presentan una destacada diversidad bioclimática y fitogeográfica, las biocostras siguen siendo un actor ecológico poco estudiado. Por ello, consideramos valioso revisar el conocimiento actual sobre las biocostras en el país, para poder identificar vacíos de información y establecer líneas prioritarias futuras de investigación. En este trabajo sintetizamos el conocimiento disponible sobre las biocostras en Argentina, centrándonos en su composición taxonómica, sus interacciones biológicas, sus patrones de distribución, sus respuestas a factores de estrés naturales y antrópicos, su rol en la multifuncionalidad de los ecosistemas y las técnicas de restauración basadas en biocostras. Hemos identificado varios aspectos clave que deberían ser priorizados en futuros estudios, como el avance en la clasificación taxonómica mediante herramientas moleculares para comprender mejor las interacciones biológicas y mejorar el uso de biocostras en la restauración de suelos degradados. También es necesario ampliar el conocimiento sobre las respuestas de las biocostras a factores ambientales a distintas escalas espaciales y temporales, para poder modelar escenarios futuros de cambio global. Aunque los esfuerzos de restauración basados en biocostras muestran resultados prometedores, la mayoría se desarrollan en condiciones controladas, y han de ser validados en campo. Consideramos que la diversidad de los ecosistemas áridos argentinos representa un laboratorio natural ideal para estudiar las biocostras y probar hipótesis sobre su biología y ecología.

[Palabras clave: ecosistemas áridos, biocostras, taxonomía, restauración, biodiversidad, agricultura, pastoreo, fuego]

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✉ sergio.sva@gmail.com

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Introduction

Biological soil crusts (biocrusts) are biological communities with photoautotrophic and heterotrophic organisms that develop at the soil-atmosphere interface, closely interacting with soil particles in the uppermost millimeters or directly on the topsoil surface (Weber et al. 2022). These communities are often classified according to the dominant community of primary producers they present: cyanobacteria, eukaryotic algae, lichens or mosses (García-Pichel 2023). Heterotrophic bacteria, archaea, filamentous fungi, mycorrhizae and microarthropods are also part of biocrusts (Belnap et al. 2016). Biocrusts occur in all terrestrial biomes, but are particularly relevant in drylands, where sparse vegetation allows solar radiation to reach the soil surface (Belnap 2003). Biocrusts are considered a multifunctional component in drylands (García-Pichel 2023), playing key roles in various ecosystem processes related to water, nutrient, energy and gas cycles (Belnap et al. 2016), and significantly influencing human well-being (Rodríguez-Caballero et al. 2018a). Biocrusts provide soil fertility as they fix atmospheric carbon (Dou et al. 2024) and nitrogen (Rodríguez-Caballero et al. 2018b), and play a central role in soil phosphorus cycling (García-Velázquez et al. 2022), a limiting nutrient in global drylands (Delgado-Baquerizo et al. 2013). Biocrusts control soil water dynamics (Eldridge et al. 2020), which has important implications for plant productivity (Antoninka et al. 2020) and, consequently, for grazing, the most important economic income for human societies in drylands (Maestre et al. 2022). Biocrusts act as a switch between solar radiation absorbance and reflection (Xiao and Bowker 2020), regulating soil surface temperature (Couradeau et al. 2016). Besides, they bind soil particles together, enhancing soil stability (Belnap and Büdel 2016), and contribute to partially alleviating the pernicious effects of soil degradation and erosion, which are among the most severe consequences of desertification in drylands (Sterk and Stoorvogel 2020).

Over the last 40 years, there has been an increasing interest in the study of biocrusts, as evidenced by two monographic books (Belnap and Lange 2001; Weber et al. 2016) and five international congresses (Germany 2010, Biological Soil Crusts in Ecosystems: their Diversity, Ecology, and Management; Spain 2013, Second International Workshop on Biological Soil Crusts: Biological Soil Crusts in a Changing World; USA 2016, The Third International Workshop on Biological Soil Crusts; Australia 2019, The Fourth International Workshop on Biological Soil Crusts; Mexico 2024, The Fifth International Workshop on Biological Soil Crusts: Systems Within Systems). However, there is a marked asymmetry in the geographical distribution of studies on biocrusts. Regions such as the USA, Australia and China have seen the vast majority of work carried out, with Spain joining this select group around 15 years ago (Maestre et al. 2011). In contrast, Argentina is beginning to study biocrusts (Figure 1). This is particularly striking considering that drylands

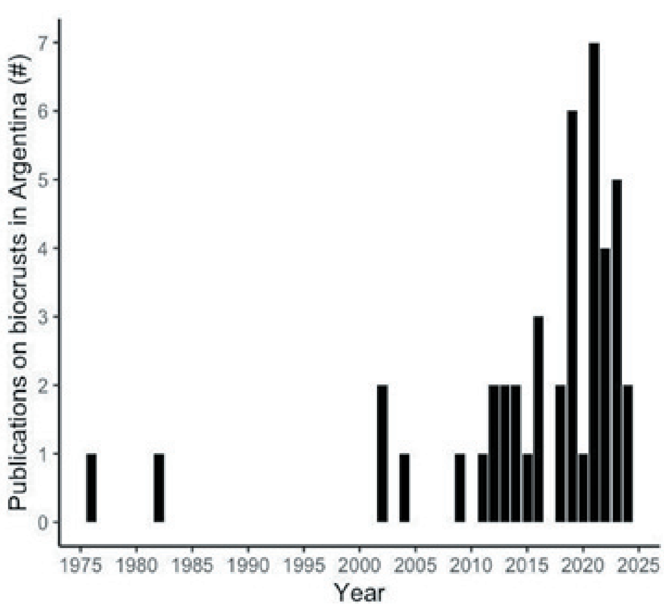

Figure 1. Annual number of publications on biocrusts in Argentina over the last five decades (n=45).
Figura 1. Número de publicaciones anuales de trabajos sobre biocostras en Argentina durante las últimas cinco décadas (n=45).

cover ~75% of the Argentine territory, with dry forests, shrublands, grasslands and high altitude deserts (Torres et al. 2015) that show contrasting Mediterranean and Monsoon precipitation regimes, cold and warm temperature regimes or large daily and monthly thermal amplitude regimes (Abraham et al. 2020). The bioclimatic and phytogeographic diversity of Argentinean drylands makes the country a natural laboratory for studying the biology and ecology of biocrusts across environmental gradients over relatively short geographical distances. In addition, the vulnerability of Argentinean drylands to desertification, driven by economic activities such as traditional grazing husbandry, pastoralism, oasis agriculture, and increasing mining and oil extraction (Torres et al. 2015), makes the study of biocrusts urgent, as biocrusts are ecosystem engineers in drylands (Xiao et al. 2022).

In this review, our goals are to 1) provide an overview of recent and current research on biocrusts in Argentina; 2) show aspects of biocrust biology and ecology that must be prioritized in future studies, and 3) demonstrate the potential of Argentinean drylands to enhance our understanding of the biology and ecology of biocrusts.

Taxonomy and Composition of Biocrusts in Argentina

The term biocrust was coined in the 1980s to describe the intimate association between soil particles and a diverse community of photoautotrophic and heterotrophic components (Weber et al. 2022). In the following years, numerous studies have described the diversity and composition of biocrusts, treating them as a geobiological assemblage (García-Pichel 2023). The taxonomic diversity of biocrusts presents a challenge for the comprehensive identification of their components, which include both microscopic and macroscopic taxa.

In Argentina, the initial studies on biocrusts focused on the taxonomy of cyanobacteria, eukaryotic algae, lichens and mosses of dryland soils. These biological components were studied as separate populations, making it difficult to determine whether the described taxa of these first works truly belonged to biocrusts. Some of the earliest studies on biocrusts in Argentina were carried out in flood-prone areas and, as a result, the microbial communities described may not fully align with the current definition of biocrusts (Weber et al. 2022). Halperín et al. (1976) examined soil cyanobacterial communities of ‘algal bioderms’ and identified numerous terrestrial taxa within the Cyanophyceae family, describing their ecology, habitat and biogeography. Additionally, they identified taxa within the Oscillatoriaceae, Nostocaceae, Scytonemataceae and Chroococcaceae families as primary components of these communities. This work highlighted the presence of numerous members of the *Microcoleus* genus, known for their thick sheaths and abundant extracellular polymeric substances. *Microcoleus* is now considered to be one of the most important cyanobacterium genus in biocrusts worldwide (Rosentreter et al. 2007) and has been consistently observed in the majority of studied biocrusts in North America and Europe, which demonstrates its central role as a pioneer in soil consolidation and biocrust formation (García-Pichel 2023). However, in other algal bioderms described by Halperín (1969), *Coelofasciculo chthonoplastes* was identified as the dominant cyanobacterium, suggesting some particularities of the regional biocrusts that distinguished them from those of other regions of the world.

Since 2010, new lines of research on the taxonomy of biocrusts have been developed in the country. As part of these efforts, other cyanobacterial taxa have been identified in drylands of Argentina. Certain taxa (e.g., *M. vaginatus*, *Nostoc commune*, *Desmonostoc muscorum* and *Phormidesmis mollis*) have been consistently described (Corvalán Videla et al. 2018; Navas Romero et al. 2020). Interestingly, several species have been reported only once, likely due to the limited geographic areas where biocrusts were sampled or the lack of extensive taxonomic and morphological studies (Navas Romero et al. 2020). Other studies have expanded the taxonomy of edaphic Cyanophyceae but, as they refer to soil cyanobacteria, in a broad sense (Díaz et al. 2022), or are based on deep soil samples, the described organisms might not necessarily constitute biocrusts (Schinquel et al. 2018; Murialdo et al. 2019; Daga et al. 2024).

Although green algae can play a more significant role than cyanobacteria (Samolov et al. 2020), their presence in Argentinean biocrusts is unexplored. Similarly, non-lichenized fungi and other heterotrophic microorganisms —which are also components of biocrusts (Maier et al. 2016)— remain poorly studied in biocrusts of Argentina. This generates uncertainty about whether they are permanent members of biocrusts or merely transient, linked to moisture-rich temporal conditions. For example, only one study has explored the heterotrophic bacterial community of biocrusts in Argentina, using the denaturing gradient gel electrophoresis (DGGE) technique (Olivera et al. 2016). This study revealed dominant microorganisms belonging to the Sphingobacteria, Solibacteres, Gammaproteobacteria and Betaproteobacteria classes. However, the DGGE approach is no longer the preferred culture-independent technique for microbial diversity and taxonomic studies, as second- and third-generation sequencing techniques have become cutting-edge methods. Molecular biology techniques enhanced both the accuracy and speed of species identification in biocrusts, as demonstrated in recent studies (Machado de Lima et al. 2021; dal Ferro et al. 2024). We consider that it is important to apply next-generation sequencing techniques targeting the 16S and 18S rRNA genes to explore and describe the composition, richness, and diversity of microorganisms in biocrusts of Argentina. To date, there are only two studies describing the composition of the microbial community of biocrusts in Latin America using this technique (Machado de Lima et al. 2019; Giraldo-Silva and Masiello 2024).

Regarding lichens, in 2002, Calvelo and Liberatore published an updated list of lichen species in Argentina, which included taxa that grow on the soil surface. This list served as a valuable starting point for identifying species present in biocrusts. Since this publication, there has been a notable increase in works on the diversity of biocrust-forming lichens in Argentina. Among the relevant studies focused on lichens, those by Scutari et al. (2002, 2004) are notable because various species from a wide variety of lichen families in biocrusts of the Patagonian steppe were described for the first time. New records of the Verrucariaceae family were provided by Prieto et al. (2008a,b) in studies carried out in northern Argentina. Recent works describing the lichen diversity of biocrusts identified Verrucariaceae, Collemataceae, Lichinaceae and Peltulaceae as the most abundant families (Scutari et al. 2004; Garibotti et al. 2018; Guiamet et al. 2019), with *Catapyrenium*, *Endocarpon*, *Enchylium*, *Heppia*, *Peltula*, *Placidium* and *Psora* as the most diverse and frequent genera (Filippini et al. 2024). These genera have a wide geographic distribution and have been found in several drylands worldwide (Rosentreter et al. 2007; Eldridge and Delgado-Baquerizo 2019). Nevertheless, the list of lichen species present in biocrusts of Argentina is more extensive, as showed by Corvalán Videla (2019), Navas Romero (2019) and Navas Romero et al. (2020) in their works on lichen-dominated biocrusts in the Monte phytogeographical province of Mendoza and San Juan provinces. It is noteworthy that many lichen observations have only been identified to the genus level, highlighting the difficulties in the identification of the species due to the scarcity of specialists dedicated to the study of lichen-dominated biocrusts and the lack of taxonomic keys developed for regional and local species.

Various works have documented the taxonomy and diversity of bryophytes in biocrusts of Argentina, particularly in the Monte phytogeographical province, where the family Pottiaceae is notably abundant. For example, Navas Romero et al. (2020) identified *Bryum argenteum* and *Pseudocrossidium arenicola* as the most abundant moss species in biocrusts along an aridity gradient in San Juan and Mendoza provinces. *Didymodon vinealis* was identified as the most dominant moss species in biocrusts after grazing abandonment in a location within the Monte phytogeographical province of the Mendoza province (Gómez et al. 2012). In the same area, Tabeni et al. (2014) identified *Tortula inermis* and *Crossidium* spp. as the main moss species present in biocrusts following grazing cessation. In the southern area of the Monte phytogeographical province, in the Río Negro province, Funk et al. (2014) and Kröpfl et al. (2022) identified *Syntrichia princeps* and *Ceratodon purpureus* as the most abundant species in moss-dominated biocrusts in two studies focused on plant germination responses to the presence of undisturbed biocrusts. In the northwestern region of Patagonia, Bustos et al. (2022) compared the differences in composition of moss-dominated biocrusts between mounds and intermounds, and found that *Tortula inermis* and *Syntrichia ruralis* are the two most abundant species, along with *Encalypta vulgaris* and *Bryum argenteum*. Velasco Ayuso et al. (2020) identified *Syntrichia caninervis*, *S. ruralis*, and *Tortula inermis* as the main bryophyte species in the Patagonian steppe of the Chubut province. Jiménez et al. (2020) identified *Aloina rigida*, *Didymodon umbrosus*, *Pseudocrossidium arenicola*, and *Trichostomum brachydontium* as the main bryophyte species in moss-dominated biocrusts of the dry Chaco phytogeographical province. Jiménez et al. (2010) described a new species, *Didymodon oedocostatus*, in the Monte phytogeographical province of Tucumán and Catamarca provinces. Schiavone and Suárez (2009) described a new moss species, *Globulinella halloyi* (Pottiaceae family), in a work carried out in the Puna phytogeographical province, near the Socompa Volcano (Salta province).

The Patagonia phytogeographical province is known for its biodiversity of terrestrial bryophytes, with 235 species recorded in a recent taxonomic inventory (most of them associated with wet meadows and lotic ecosystems, and only a few found in the vast semiarid steppe) (Cottet 2023). Cottet and Messuti (2023) described 43 terrestrial moss species for the first time in the Argentinean Patagonia, highlighting how little we know about the true diversity of mosses in our drylands, and even less about which of these mosses are part of biocrusts. Our limited knowledge of soil bryophyte diversity in Patagonia clearly reflects the uneven distribution of biocrust studies in Argentina, which show a higher concentration in the central-northern regions of the country compared to the southern part (Figure 2).

Here, we present a list of "cyanobacteria" lichens, and bryophytes identified in Argentinean biocrusts to date (Supplementary Material-Table S1). However, we acknowledge that this list is far from complete. The knowledge about the taxonomic composition of biocrusts is greater in other drylands of the world than in Argentina (Maestre et al. 2011; Li et al. 2021; Warren et al. 2021). In Mexico, for example, 200 different species have been identified in biocrusts, including 61 cyanobacteria, 51 lichens, 26 bryophytes, 47 algae and 15 fungi (Sosa-Quintero et al. 2022). In Brazil, 49 cyanobacteria, 8 lichens, 10 bryophytes and 12 algae have been reported to belong to biocrusts (Oliveira and Maciel-Silva 2022). To improve our knowledge of biocrust

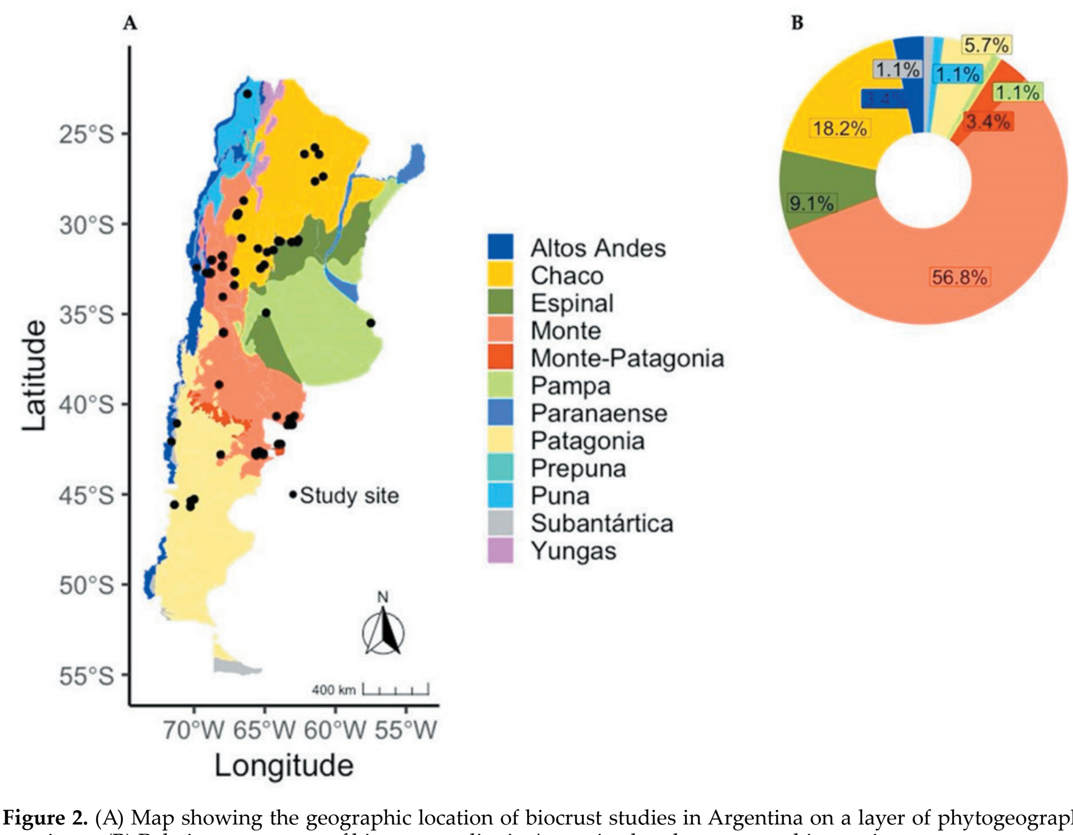

Figure 2. (A) Map showing the geographic location of biocrust studies in Argentina on a layer of phytogeographic provinces. (B) Relative percentage of biocrust studies in Argentina by phytogeographic province.

Figura 2. (A) Mapa que muestra la localización geográfica de los estudios de biocostras en Argentina sobre una capa de las provincias fitogeográficas. (B) Porcentaje relativo de estudios de biocostras en la Argentina por provincia fitogeográfica.

composition in Argentina, it is essential to have guides, floras and regional identification keys, at least for macroscopic organisms such as bryophytes and lichens. In Argentina, only a few taxonomic studies on biocrust composition have been published, and no regional identification keys are available. We therefore rely on keys developed for other regions of the world, which are often not comparable. Because biocrust responses to global change and the success of restoring degraded dryland soils depend on community composition, we strongly recommend that biocrust researchers in Argentina collaborate with taxonomists to develop regional identification keys. These keys will help us complete the lists of biocrust taxa at a regional scale.

Community Ecology Within Biocrusts

Interactions among biocrust components have emerged as a significant field of research over the past decade (Maestre et al. 2011). However, only a limited number of studies have addressed this topic (Maestre et al. 2008, 2009), and none of them was carried out in Argentina.

Interactions between biocrust components occur from the very beginning of biocrust community assembly and are context dependent. For example, the development of cyanobacteria-dominated biocrusts in dryland soils is often facilitated by the association of cyanobacteria with specific heterotrophic organisms, which involves the exchange of carbon and nitrogen compounds (Nelson and García-Pichel 2021). Regarding lichens, various studies conducted in central Spain showed that competition is more intense than facilitation in assembling lichen-dominated biocrust; this intensity decreases or increases depending on whether water or nutrients are the main limiting resource, respectively (Maestre et al. 2008, 2009). Similarly, Bowker et al. (2010) found that negative interactions between species prevailed in lichen- and moss-dominated biocrusts, and that the intensity of competition increases with increasing abiotic stress. Bowker et al. (2010) also observed that competition was positively or negatively related to species richness under low and high abiotic stress conditions, respectively. Nevertheless, competition among biocrust species is modulated by microsite conditions and plays a major role in biocrust community assembly beneath plants, compared to open areas between plant patches (Soliveres and Eldridge 2020). Although competitive exclusion has been rarely described in bryophyte communities, this is not due to a lack of competition, but rather a balance between competition and facilitation (During and Lloret 2001). Few cases of facilitation were found among the components of biocrusts, but lichens and bryophytes produce a wide variety of chemicals, some of which are essential in nutrient absorption or defense. Thus, species with complementary chemical compounds can benefit from association (Maestre et al. 2011). In some cases, parasitism occurs among soil lichens, where a mycobiont can steal the photobiont of other species. For example, *Diploschistes muscorum* begins its thallus development as a parasite of *Cladonia* spp., eventually outcompeting the original lichen. In this scenario, the host is facilitating the development of the parasite species (Friedl 1987; Schaper and Ott 2003). However, it is important to realize that facilitation and competitive mechanisms among biocrust lichens and mosses are different from vascular plants because, as two-dimensional organisms, biocrust components exhibit little overlap (Bowker et al. 2010).

The study of the interactions among components of biocrusts is likely one of the key issues that must be addressed in the drylands of Argentina. Only by understanding how biocrust taxa interact with one another will we be able to comprehend how biocrusts will respond to changes in land use or climate. Furthermore, gaining insight into these interactions could aid in the design of restoration projects aimed at recovering biocrust biodiversity and their associated ecosystem functions and services. The diversity of structural types of biocrusts found in Argentinean drylands (Figure 3), along with the variety of climates, represented, for example, by the aridity index, makes the country a natural laboratory to study the interactions between biocrust components.

Interactions Between Biocrusts and Plants

The coexistence of biocrusts and plants has been recognized as a stable state in global drylands, with key implications for ecosystem functioning (Chen et al. 2020). The tight interaction between biocrusts and plants determines the spatial functional organization of drylands (Kozar et al. 2024). As such, the

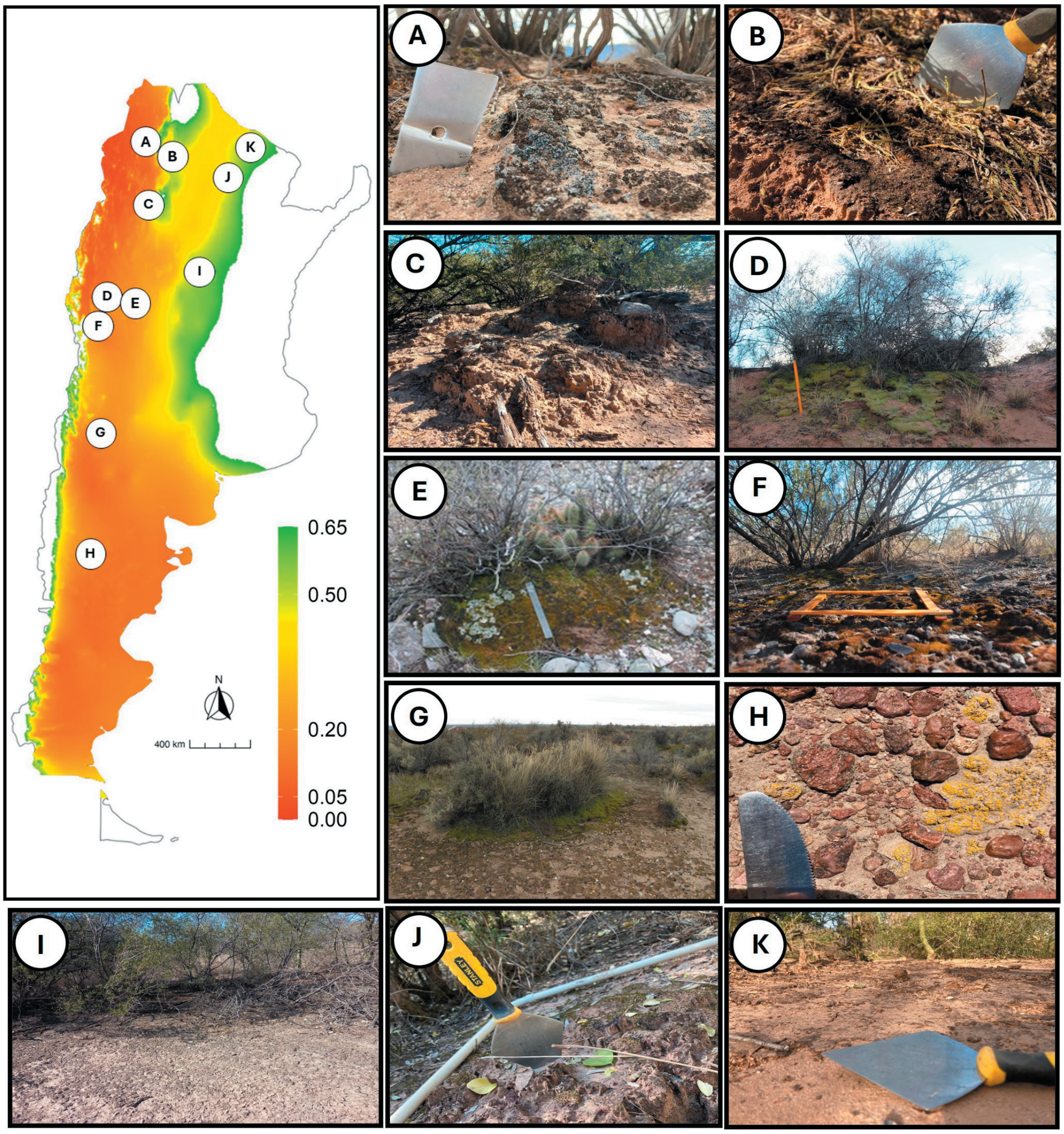

Figure 3. Photographs of biocrusts in Argentina (A-K). The sites where the photographs were taken are located on an aridity index layer that represents the aridity levels of drylands (the aridity index —AI— is calculated as the ratio of annual mean evapotranspiration to annual mean precipitation (UNEP 1992); hyper-arid, AI<0.05; semi-arid, 0.05<AI<0.2; arid, 0.2<AI<0.50; dry subhumid, AI>0.50).

Figura 3. Fotografías de las biocostras en la Argentina (A-K). Los sitios donde se tomaron las fotografías están ubicados sobre una capa de índice de aridez que representa los niveles de aridez de los ecosistemas áridos (el índice de aridez —IA— se calcula como la relación entre la evapotranspiración media anual y la precipitación media anual (UNEP 1992); hiper-árido, IA<0.05; semiárido, 0.05<IA<0.2; árido, 0.2<IA<0.50; seco subhúmedo, IA>0.50).

study of the interaction between plants and biocrusts is a topic that has attracted increasing research interest over the years to better understand the functioning of drylands (Bowker et al. 2022). On the one hand, the study of plant-biocrust interactions has been largely based on experimental and observational approaches comparing the performance of early stages of plant establishment in the presence or absence of biocrusts. Significant interspecific variation in plant responses to biocrusts has been found, mostly depending on biocrust type, plant traits, plant ontogeny stage and environmental conditions (Havrilla et al. 2019). Biocrusts can also influence plant community assembly by differentially selecting some species over others, and by inducing priority effects, although the effects vary depending on the attributes of the biocrust community (Bowker et al. 2022). On the other hand, how plants shape biocrust communities has been mostly assessed by comparing biocrusts in plant interspaces to those beneath plant canopies (Eldridge et al. 2010). Some studies found that biocrust growth is inhibited under plant canopies, likely due to the accumulation of large quantities of litter, light and water canopy interception, soil resources competition, and production of allelopathic substances (Bowker et al. 2016; Zhang et al. 2016; Mallen-Cooper et al. 2022). However, enhanced biocrust cover and/or richness below plant canopies has also been reported, probably related to microclimatic amelioration and protection from disturbance, especially grazing (Berkeley et al. 2005; Ochoa-Hueso et al. 2011; Tabeni et al. 2014; Soliveres and Eldridge 2020).

There are 17 studies focused on plant-biocrust interactions in Argentina, either based on field studies or experimentation in greenhouse facilities. Research on the spatial associations between biocrusts and vascular plants has been used to understand the effects of plants on biocrusts across various disturbance contexts, including comparisons between grazed and ungrazed areas or sampling at different distances from human settlements and water points. All these studies were performed in the central region of Argentina, mainly in the shrubby steppe of the Monte phytogeographical province. Results evidenced the positive effect of vascular plants in protecting biocrusts from trampling, with higher biocrust cover values beneath the plant canopy compared to open interspaces (around 13 and 4%, respectively) (Gómez et al. 2012). Biocrusts are preferentially distributed beneath fine-leaved shrubs, probably because this kind of plants improves microclimate conditions, allows light to diffuse to the soil surface and produces relatively low amounts of litter (Gómez et al. 2012; García et al. 2015). In contrast, biocrusts and grasses show a positive interaction in highly disturbed environments caused by grazing and heavy machinery (Kröpfl et al. 2022), but, as the intensity of the disturbance decreases, the interaction becomes negative (Tabeni et al. 2014).

Some regional studies showed that vascular plants alter niche-based community assembly patterns of biocrusts, leading to the dominance of mosses over lichens beneath plant canopies and significant differences in the relative cover of biocrust species compared to open spaces (Gómez et al. 2012; Bustos et al. 2022). Large-scale analyses showed that the association of moss-dominated biocrusts with vascular plants increases along an aridity gradient, while lichen-biocrusts were associated with vascular plants only in hyper-arid drylands (Navas Romero et al. 2020). Cyanobacteria-dominated biocrusts are usually not associated with vascular plants (Gómez et al. 2012; Navas Romero et al. 2020).

Another line of research on plant-biocrust interactions focuses on how different stages of the vascular plant life cycle respond to the presence of biocrusts. Studies conducted in the Patagonia and Monte phytogeographical provinces analyzed the natural distribution pattern of the soil-seed bank, finding larger and more diverse soil-seed banks of palatable perennial grasses in lichen- and moss-dominated biocrusts than in nearby bare soil areas, which suggests that biocrusts act as seed traps (Bertiller and Ares 2011; Kröpfl et al. 2022; Kröpfl 2023). Greenhouse and field experiments on the effects of biocrusts on seedling emergence, growth and survival have been conducted for different plant growth forms (grass, shrub and tree). Emergence and growth of grass seedlings has been found to be neutral or negative in soils with moss-dominated biocrust compared to bare soils under field or no-watering conditions, but positive when soil moisture was maintained at field capacity (Funk et al. 2014; Zeberio and Peter 2021; Kröpfl et al. 2022; Kröpfl 2023). However, Corvalán Videla et al. (2021) found positive effects of different biocrust types on grass seedlings under watering conditions. The positive effects of biocrusts on grass seedlings found by Corvalán Videla et al. (2021) were due to modifications in soil carbon, nutrient, and water dynamics. This resulted in increased seedling emergence and biomass, as well as decreased nutritional values, estimated as leaf carbon-to-nitrogen ratios. Two greenhouse studies evaluated the effect of moss-dominated biocrusts on different shrub species. One study found depressed seedling emergence (Peter et al. 2016), while another observed species-specific differences in seedling growth, likely influenced by the impact of biocrusts on the availability of different nitrogen forms (Garibotti et al. 2023). Finally, the only study focused on a tree species found an increased seedling emergence in bio-crusted soils compared to bare soils (Calabrese and Rovere 2013).

Overall, various studies in Argentina showed strong positive or negative effects of interactions between biocrusts and plants, whether plants influence biocrusts or vice-versa. Results showed that the outcome of these interactions varies depending on the biocrust type, plant life form and life stage, and is shaped by environmental conditions and disturbance regimes. Biocrust-plant interactions are therefore difficult to generalize, as previously evidenced by Havrilla et al. (2019) in a global meta-analysis. Hence, we need to conduct further studies on these interactions by expanding them to more Argentinean drylands, including a greater number of plant species and additional structural types of biocrusts. Studies that include both experimental and natural observations must be prioritized, as both approaches contribute to fully evaluating these interactions. Increasing our understanding of biocrust-plant interactions goes beyond the basic research interest, as it has many implications for ecological conservation, restoration and economic development. As our comprehension of biocrusts in drylands has improved over the last decades, the traditional plant-centered model of dryland dynamics has shifted toward a more integrated perspective that recognizes drylands as a mosaic of biocrusts and plants. In this context, efforts are being made to implement conservation and restoration practices that consider the need to preserve, maintain and recover the biocrust-plant interactions at the landscape scale (Bowker et al. 2022; Maggioli et al. 2022). Finally, studies on biocrust-plant interactions in Argentina have been mostly performed in rangelands. However, recent works highlight the relevance of these interactions in agricultural systems too, with potential economic impacts (Kurth et al. 2023), as biocrusts may be a natural fertilizer, thus contributing to new agroecological initiatives (Kurth et al. 2023).

Natural Factors that Determine Patterns of Biocrust Distribution

Spatial distribution patterns of biocrusts have been studied over the last decades, and we now know that climatic, topographic, edaphic, and biotic factors control biocrust distribution at various scales in drylands, from global to continental, regional and local (Bowker et al. 2016). At a local scale, fine soil particles are associated with higher cover and diversity of biocrusts (Rozenstein et al. 2014; Castillo-Monroy et al. 2016). At a regional scale, the spatial distribution of biocrusts is associated with topographic variables, with slopes receiving incoming solar radiation showing the highest cover values of biocrusts (Rodríguez-Caballero et al. 2019). At a continental scale, climatic and geographic variables determine the structure and functioning of biocrusts (Bowker et al. 2016). For example, Eldridge and Tozer (1997) found that lichen diversity was related to annual mean rainfall in Australian drylands. Qiu et al. (2023) recently demonstrated that biocrust cover positively responds to the aridity index while negatively to the altitude across drylands of China. Rodríguez-Caballero et al. (2018b) found that mean temperatures of the driest quarter and precipitation amounts of the warmest quarter of the year are associated with higher cover values of biocrusts in global drylands. At a global scale, three studies have defined the relationships between biocrust cover, climate, and the functional role of biocrusts in the carbon and nitrogen cycles, as well as in the global dust cycle (Elbert et al. 2012; Rodríguez-Caballero et al. 2018b; Rodríguez-Caballero et al. 2022).

In Argentina, at a local scale, Velasco Ayuso et al. (2020) found low biocrust cover values (1-2%) in the Patagonian steppe of the Chubut province, compared to those found in areas of the Monte phytogeographical province (8-60%; Calabrese et al. 2013; García et al. 2015; Navas Romero et al. 2020; Bustos et al. 2022; Kröpfl et al. 2022). They attributed this finding to the presence of coarse-to-medium sands, among other factors. As we mentioned earlier, plants have a significant influence on the distribution of biocrusts, controlling variability at both local (e.g., plant patches versus open microsites) and regional (e.g., differences between vegetation communities) scales. Tabeni et al. (2014) observed that plant cover positively determines the cover of biocrusts at a local scale in the Monte phytogeographical province of the Mendoza province. In Telteca Natural Reserve (Monte phytogeographical province, Mendoza province), García et al. (2015) found larger biocrust patches below the canopy of plants than in open, interpatch areas. Additionally, Calabrese et al. (2013) observed that plants provide protection against trampling, wind and sunlight radiation, thereby facilitating the presence of relatively larger patches of biocrusts in the Patagonia phytogeographical province of the Río Negro province. At a regional scale, in drylands of the Mendoza province, García et al. (2015) found that topography controls the presence of biocrusts, with higher cover values in old riverbed areas compared to aeolian flat areas, probably because of a reduced effect of water and aeolian erosion rates. Unfortunately, large-scale studies focused on the factors that control the structure and functioning of biocrusts in Argentina are lacking. Navas Romero et al. (2020) provide the only available description of how biocrust cover and species richness vary along an aridity gradient in the Monte phytogeographical province, showing higher biocrust cover in arid sites compared to semiarid and hyper-arid areas (42, 21 and 25%, respectively).

It is important to perform large-scale studies on biocrusts in Argentina, like those conducted in China (Qiu et al. 2023), Australia (Eldridge and Tozer 1997) or the USA (Condon and Pyke 2020), as this information will improve our comprehension of the role of biocrusts in the structure and functioning of drylands at a subcontinental scale. Given the key role that biocrusts play in global carbon and nitrogen cycles (Elbert et al. 2012), as well as in the global dust cycle (Rodríguez-Caballero et al. 2022), and considering that Earth System Models (ESMs) are built upon climate models, it is essential to understand how biocrust structure and function respond to climate. Argentina is a country with a wide variety of climates, and changes in both mean and extreme temperature and precipitation values are currently underway. To advance our understanding of climate-biocrust relationships at the Argentinean scale, we must use climate (e.g., WorldClim, TerraClimate, CHELSA) and land use (e.g., WorldCover, GlobalDynamicLandCover) products to better determine the role of biocrusts in the functioning of drylands under present conditions. With this knowledge, we will be able to better predict how changes in temperature, evapotranspiration, precipitation or land use will impact biocrusts, allowing us to determine how global change will affect biocrust structure, functioning, and ecosystem services they provide. We can use the bioclimatic diversity of drylands in Argentina as a natural laboratory to define these climate-biocrust relationships, providing valuable data to the scientific community to improve the accuracy of predictive models by taking into account the compartment of biocrusts, which, as we have already explained, form the soil-atmosphere interface in dryland soils, and probably play a significant role in ESMs. It is surprising that model-based global distribution maps of biocrusts, such as moss-dominated biocrusts, for example, consistently lack field observations from Argentina (Eldridge et al. 2023). It is time to reverse this situation by fostering field trips and collaborations with regional climate scientists and modelers.

Anthropogenic Factors that Determine Patterns of Biocrust Distribution

Despite their resilience to extreme natural conditions, such as high temperatures, low precipitation rates and intense UV radiation, biocrusts are significantly threatened by various anthropogenic-induced stress factors. Trampling by domestic animals, which exerts compressional forces that destroy their integrity and detach them from the soil surface, is perhaps the most critical human-related stress factor controlling the structure and functioning of biocrusts in global drylands (Zaady et al. 2016). Fire represents another significant disturbance factor for biocrusts. The resistance of biocrusts to fire and their recovery after fire events are currently topics of interest, as biocrusts are considered to be ecosystem engineers (Brianne et al. 2020). The response of biocrusts to climate change has also gained interest in recent years due to significant observed biocrust mortality rates and a shift from late-successional moss-dominated communities to early-successional cyanobacteria-dominated communities, as both phenomena are associated with a reduction in ecosystem services provided by biocrusts (Reed et al. 2012; Ferrenberg et al. 2015).

In Argentina, there are numerous studies that have evaluated the response of biocrusts to grazing. In dry sub-humid grasslands of Argentina, Ansín et al. (2002) found that grazing decreased the abundance of *Nostoc* (from 17 to 5%), a pioneering cyanobacterium with a central role in the initial steps of the establishment and development of biocrusts. Bertiller and Ares (2011) found negative effects of plant selectivity by sheep on the cover of biocrusts in the Monte phytogeographical province. Cheli et al. (2016) observed that sites located farthest from water points in Península Valdés (Monte phytogeographical province, Chubut province) exhibited the highest biocrust cover values, which indicates a piosphere effect provoked by the presence of sheep; these authors reported that the cover of biocrusts decreased by half near the watering point compared to the cover found at 3000 m. Plants, however, serve as refugia for biocrusts against trampling. For example, Calabrese et al. (2013) found in drylands of the Río Negro province a higher diversity and cover of biocrusts in grazed areas, compared to fenced areas, but always below the canopy of plants, not in open areas. In fact, grazing, or the combined effect of grazing and mechanical removal of plants, negatively impacted on the cover of moss-dominated biocrusts in north-eastern Patagonia (Kröpfl et al. 2022). After grazing cessation, the establishment and development of biocrusts naturally occur in drylands of Patagonia (Velasco Ayuso et al. 2024). Funk et al. (2012) found that excluding grazing for 10 years led to the reestablishment of biocrusts in Patagonian semiarid rangelands. Gómez et al. (2012) found that biocrust cover naturally recovers following grazing abandonment in the Monte phytogeographical province, with cyanobacteria- and lichen-dominated biocrusts showing higher cover values in inter-patches than in plant patches, and with moss-dominated biocrusts showing similar values between both microsites. Velasco Ayuso et al. (2020) found that grazing abandonment was associated with significant increases in biocrust biomass, total cover and diversity of structural types within approximately 20 years in the Patagonian steppe of the Chubut province. To partially mitigate the pernicious effects of sheep grazing on biocrusts, Velasco Ayuso et al. (2020) proposed that light-grazed fields are preferable over high-grazed fields and that high-grazing intensities should be avoided under high aridity conditions.

Extensive agriculture represents another major threat to biocrusts in Argentina. Tillage-based farming directly removes biocrusts, leading to the loss of soil stability, decreased fertility and increased aeolian and hydric erosion rates (Ferrenberg et al. 2015). In the Monte phytogeographical province, the conversion of natural lands into croplands has resulted in significant reductions of biocrust cover (Paruelo et al. 2006). Furthermore, agrochemical applications, such as herbicides and fertilizers, alter microbial communities within biocrusts, reducing their capacity for nitrogen fixation and soil nutrient enrichment (Denegri et al. 2021). These results suggest the need for conservation tillage techniques and the establishment of buffer zones to preserve the integrity of biocrusts in croplands.

Desertification, a growing concern in Argentina, further exacerbates the decline of biocrusts. Approximately 75% of drylands is affected by soil degradation processes, largely driven by human-induced factors such as deforestation, high-intensity land use and climate variability (Zabala et al. 2023). In Patagonia and Monte phytogeographical provinces, soil degradation has been linked to reduced biocrust diversity and functionality, and increasing aridity has been shown to limit recovery rates of biocrusts (Velasco Ayuso et al. 2020). The spread of invasive plant species, such as *Tamarix gallica*, also poses a challenge by outcompeting native vegetation and altering soil properties, further inhibiting biocrust re-establishment (Funk et al. 2012). To mitigate the impact of desertification on biocrusts, various management strategies have been proposed. Sustainable grazing practices, including rotational grazing and exclusion zones, have shown positive effects in maintaining biocrust stability while allowing grazing production (Gómez et al. 2012; Kröpfl et al. 2022). In croplands, conservation tillage, reduced chemical input and the maintenance of natural vegetation corridors can help minimize soil disturbance and preserve microbial diversity (Ferrenberg et al. 2015; Denegri et al. 2021). Additionally, land restoration programs, such as the active reintroduction of biocrusts in degraded areas, are promising techniques for accelerating biocrust recovery in drylands. All these approaches, combined with policy frameworks that integrate biodiversity conservation into land-use planning, are essential for ensuring the long-term persistence of biocrusts in drylands of Argentina.

Regarding the impact of fire on biocrusts, a factor that permanently affects large regions in Argentina, three studies have been conducted to date. In central-west Argentina, Denegri et al. (2021) found that cyanobacteria-dominated biocrusts responded differently to fires, and concluded that the responses were related to the intensity of the fire event. In the same area, within the Chaco phytogeographical province, Perazzo and Rodríguez (2019) found low cover values of lichen- and moss-dominated biocrusts 15 years after the fire. Zabala et al. (2023) observed that the abundance of cyanobacteria- and lichen-dominated biocrusts varied depending on the time post-fire, with cyanobacteria-dominated biocrusts showing faster recovery rates than lichen-dominated biocrusts.

Unfortunately, no large-scale studies to assess the potential impacts of climate change on biocrusts have been carried out in Argentina to date. At a local scale, however, the study by Velasco Ayuso et al. (2020) in the Patagonian steppe of the Chubut province examined the variation in the development and diversity of biocrusts along a precipitation gradient and demonstrated that negative effects of grazing on biocrusts are more pronounced under high aridity conditions.

Compared to other global drylands, we have a reasonably good level of knowledge about the effects of anthropogenic-related stress factors on the distribution of biocrusts in Argentina. However, there is no doubt that improving our understanding of the impact of grazing on biocrusts should be a priority since most drylands in Argentina have a long history of land use for grazing. In addition, assessing the response of biocrusts to fire must be a priority in Argentina, particularly as climate change is anticipated to change fire patterns (Zhang et al. 2024), with significant implications for dryland soils. Climate change will impact Argentinean drylands (Hurtado et al. 2023), exacerbating the negative effects of desertification (Torres et al. 2015), which emphasizes the need for further research on these topics. The expansion of the agricultural frontier in Argentina represents another stress factor for biocrusts, especially because this expansion mainly occurs in drylands (del Giorgio et al. 2022), and its effects have not been fully evaluated yet. Intensive land use involves contrasting interests: on the one hand economic activities threaten biocrusts, while on the other hand biocrusts provide valuable ecosystem services. However, society is still far from recognizing the importance of services that biocrusts provide (Rodríguez-Caballero et al. 2018a). Engaging with stakeholders, social actors and policy makers remains a challenge for us as scientists, but we must try to increase their awareness of biocrusts and the importance of preserving and restoring biocrust biodiversity and functionating.

Biocrust and Ecosystem Functioning

Biocrusts play key functional roles at the soil-atmosphere interface in global drylands (Belnap et al. 2016). Biocrusts fulfill a wide range of ecological roles, particularly in modifying soil properties and regulating functions and multifunctionality (Bowker et al. 2018). A substantial body of literature has showed that biocrust functions vary depending on the composition of the community (Eldridge et al. 2010; Castillo-Monroy et al. 2011; Eldridge et al. 2021; Concostrina-Zubiri et al. 2022) and on the environmental context, including vegetation and other biotic characteristics, climate and soil properties, as well as disturbance type and level (Chamizo et al. 2009; Zhang et al. 2016; Mallen Cooper et al. 2018; Eldridge et al. 2020; Riveras-Muñoz et al. 2022). Understanding the functional roles of biocrusts requires considering their variability at local and regional scales.

In Argentina, several studies have evaluated the functional role of biocrusts in soil thermal balance, nutrient cycling, water dynamics and soil stability. It has been shown that biocrusts greatly contribute to small-scale heterogeneity in the functioning of both vegetated and unvegetated interspace microsites, having idiosyncratic effects on different key ecosystem functions (Garibotti et al. 2018). After grazing cessation, the establishment and development of moss- and cyanobacteria-dominated biocrusts significantly enhanced soil multifunctionality in the Patagonian steppe, improving soil stability (Velasco Ayuso et al. 2024). This essential functional role that biocrusts play in drylands is due to their ability to aggregate surface soil particles (García-Pichel and Wojciechowski 2009; Navas Romero et al. 2019). Greenhouse experiments have also shown that the soil stabilizing function is rapidly recovered in treatments seeded with moss-dominated biocrusts (García et al. 2021). In the Monte and Patagonia phytogeographical provinces, both biocrusts and vascular plants are multifunctional stabilizing agents, with moss-dominated biocrusts having the potential to functionally substitute vascular plants in stabilizing soils in inter-patches areas with reduced plant cover (Garibotti et al. 2018; Bustos et al. 2022). On average, a biocrust cover higher than 50% seems to be necessary for stabilizing soil surface in both vegetated and interspace areas in the Monte phytogeographical province (Bustos et al. 2022).

Biocrusts significantly control soil water dynamics by regulating rainfall infiltration and surface moisture content in drylands of Argentina. It has been demonstrated that bio-crusted soils have greater water storage capacity than bare soils, especially when they are dominated by mosses (Pissolito et al. 2019; Corvalán Videla et al. 2021; Navas Romero et al. 2021a; Kröpfl et al. 2022; Kröpfl

2023). Additionally, biocrusts with surface discontinuities may function as micro-channels, allowing water to filter into the soil (Garibotti et al. 2018). Moreover, the role of biocrusts in controlling soil moisture content is closely linked to their role in buffering soil temperature, through the regulation of water evaporation rates, with one study demonstrating that biocrusts cause a 3-7 °C decrease in mean daily soil temperature (Navas Romero et al. 2023). On the other hand, in the Monte phytogeographical province, the infiltration function greatly depends on biocrust community composition, being enhanced as the richness of biocrusts increases, probably due to the intimate associations between different components that create hydrophobic and hydrophilic patches (Garibotti et al. 2018). For example, it has been shown that increasing cover of small squamulose and crustose lichens, along with the moss *Bryum argenteum*, negatively affects infiltration (Bustos et al. 2022). In addition, infiltration rates depend on soil texture, with biocrusts exerting positive effects in loam and loam-sandy soils, and negative effects in sandy soils (Navas Romero et al. 2021a). To date, no studies in Argentina have evaluated other processes in soil water dynamics, such as water runoff and non-rainfall water sources. The latter may be critical for biocrust development in large areas of Argentina, where rainfall is below 200 mm per year. In these dryland regions, biocrusts may be active during winter, when air humidity is relatively high and dew is likely the most important —and perhaps the only— water source (Bustos et al. 2022).

Biogeochemical processes dominate the literature evaluating the effect of biocrusts on ecosystem multifunctionality in Argentina. Halperín et al. (1976) demonstrated the ability of cyanobacteria-dominated biocrusts to increase soil inorganic nitrogen availability, reaching concentrations from 1.5 to 8 times higher than bare soil areas. In the Monte and Patagonia phytogeographical provinces, biocrusts contribute significantly to soil total nitrogen enrichment in both vegetated and open microsites, but reduce the concentration of inorganic nitrogen. This suggests a tradeoff between the role of biocrusts in nitrogen storage and its cycling within the system (González Polo and Austin 2009; Gómez et al. 2012; Garibotti et al. 2018; Aranibar et al. 2022; Bustos et al. 2022). In these two phytogeographical provinces, biocrusts also play a crucial role in soil phosphorus availability. Moss-dominated biocrusts have a negative effect, while lichen-dominated communities have a positive effect on soil phosphorus pools. This illustrates a close connection between biocrust composition and the biochemical functions that regulate this essential nutrient in dryland soils (Garibotti et al. 2018; Bustos et al. 2022). Moreover, soil total carbon and the microbial carbon cycling functions are enhanced in biocrusts when compared to bare soil areas (González Polo and Austin 2009; Bustos et al. 2022; Velasco Ayuso et al. 2024). Studies evaluating biocrust development over time after grazing cessation in Patagonian rangelands showed an increasing, but non-significant, trend in biocrust multifunctionality associated with soil carbon, biogeochemical cycling and fertility (Velasco Ayuso et al. 2024). Some of the functional roles of biocrusts in soil nutrient cycling have been tested in greenhouse facilities, demonstrating that biocrusts enhance soil total nitrogen while reducing phosphorus availability. Additionally, the concentration of inorganic nitrogen depends on the type of biocrust (Corvalán Videla et al. 2021).

Several studies in Argentina have focused on quantifying biocrust functioning and multifunctionality through field and experimental research. However, most of these studies are restricted to specific biocrust communities or localized regions within this vast and diverse country. Compared to global drylands, studies on biocrust functioning and multifunctionality in Argentina need to be expanded both spatially and temporally. Expanding our understanding of biocrust-ecosystem functioning relationships would greatly benefit from considering the variability of biocrusts across Argentinean drylands, as well as their local and regional environmental contexts. To achieve this, it is essential to establish a coordinated network of biocrust scientists using homogeneous methodologies to address specific research questions.

Biocrust Restoration

Drylands are among the most threatened terrestrial ecosystems and face accelerated degradation rates due to human activities (Reynolds et al. 2017). This degradation results in the loss of vital ecosystem services and disruption of socio-ecological services (Condon et al. 2024), largely due to desertification (Burrell et al. 2020). Restoring biocrusts has emerged as a promising strategy to partially mitigate desertification given their key role as ecosystem engineers (Antoninka et al. 2020). Biocrust restoration aims not only at the biological recovery of the soil but also at promoting soil health, which is vital for ecological functioning (Muñoz-Rojas et al. 2021).

Current research focuses on developing optimal and sustainable methods for using biocrusts in ecological restoration (Schultz et al. 2022; Garibotti et al. 2023; Maleševic et al. 2024). This includes 1) optimizing cultivation techniques, 2) maximizing field survival rates, and 3) integrating various field restoration methods (Young et al. 2016; Navas Romero et al. 2021b). Inoculating degraded dryland soils with cyanobacteria has proven to be a promising technique, demonstrating success in enhancing soil stability. Cyanobacteria-dominated biocrusts produce exopolysaccharides that bind soil particles and facilitate the recolonization of other native soil taxa (Muñoz et al. 2021; Zhao et al. 2021). In other drylands, where lichen- and moss-dominated biocrusts are more abundant than cyanobacteria-dominated biocrusts, efforts have been focused on recovering these biocrusts components, but field trials have frequently failed due to the loss of lichen and moss inocula or limited growth in the long term (Rosentreter 2020). In any case, field biocrust restoration faces significant challenges, including slow recovery rates under severe conditions and the need for effective techniques to accelerate the natural restoration process (Kidron et al. 2020). Understanding all these challenges is crucial to maximize the success of restoration processes and to promote resilient, self-sustaining ecosystems in degraded drylands (Lorite et al. 2020). It is important to note that biocrust restoration is generally considered a secondary or tertiary step in ecosystem restoration. The site undergoing restoration typically needs to go through an initial recovery phase —such as fertilization, soil decompaction and stabilization— before introducing biocrusts (García et al. 2021).

In Argentina, four studies have focused on developing optimal greenhouse techniques for cultivating biocrusts. Storni de Cano (1982) conducted the first study aimed to reactivate biocrusts stored for 10 years, assess their multiplication capacity, evaluate their effect on nitrogen fixation and examine their impact on crop growth. Air-dried and crushed crusts were inoculated into sterilized native soil. After four months of growth under artificial light, the study reported a 90% surface cover on the inoculated area, along with increased soil nitrogen and improved germination of the herb *Beta vulgaris*. The study also recognized the need for field trials to validate the greenhouse findings. García et al. (2021) conducted a greenhouse study in which different functional types of biocrusts collected from the Monte phytogeographical province were cultivated. The study tested two main treatments: seeding methods (biocrusts crushed into fragments or added as larger pieces) and fertility (substrate with or without goat manure). Results showed that the crushed seeding method combined with the absence of fertilizer significantly enhanced biocrust cover and depth, leading to increased soil stability, in comparison to non-crushed biocrusts and goat manure addition. In addition, this study tested different types of biocrusts, cyanobacteria-, lichen- and moss-dominated biocrusts, and demonstrated that the positive results apply equally to all three biocrust components, thus opening the way for the development of restoration programs for degraded dryland soils that go beyond the exclusive use of cyanobacteria-dominated inocula. Additionally, García et al. (2023) evaluated the impact of various environmental conditions on the cultivation of biocrusts, including three levels of radiation (high with no shading, medium with 65% shading, and low with 80% shading), three irrigation frequencies (every three weeks, every two weeks and weekly), and two salinity levels (0.05 M and 0.1 M NaCl). They found that weekly irrigation, medium radiation levels, and the absence of salinity were conditions that maximized biocrust biomass growth. In addition, Garibotti et al. (2023) conducted a greenhouse experiment to test the effects of compost addition (sewage sludge compost, organic solid waste compost, or none), biocrust inoculation and shrub seedling planting (*Acaena splendens* or *Senecio filaginoides*) on biocrust and plant growth. Both compost types improved biocrust cover and increased contents of chlorophyll *a*, with sewage sludge compost also enhancing seedling growth. However, biocrusts had differing effects on the two plant species. The study concludes that although sewage sludge compost promotes the co-cultivation of biocrusts and plants, species-specific responses constrain the simultaneous restoration of both. All these works and efforts have centered on maximizing the survival rates of biocrust inocula during the greenhouse stage. However, it is crucial to test these results in the field to determine whether an initial amelioration phase is necessary. This second phase of the restoration process might include activities such as adding fertilizers, soil decompaction and stabilization before biocrust inoculation.

While greenhouse and laboratory cultivation of biocrusts have shown promising results, transferring grown inocula to field conditions presents significant challenges. Low survival rates of inocula, environmental variability and competition with invasive species often limit success (Antoninka et al. 2020; Bowker et al. 2022). High production costs and the need for pre-inoculation site conditioning —such as soil decompaction, organic amendments, or stabilization— are critical obstacles (Xiao et al. 2011; Faist et al. 2020). An additional strategy to improve restoration outcomes could involve the co-transfer of biocrusts with vascular plants, enhancing mutual benefits like soil stabilization and microclimatic regulation (Antoninka et al. 2020; Bowker et al. 2020). However, in Argentina, field experiments are limited and mostly restricted to the Monte phytogeographical province (García et al. 2021). Expanding field trials, adjusting inoculation densities, and exploring species-specific responses are essential actions for advancing large-scale biocrust restoration projects. Collaboration with local stakeholders and policymakers will also be crucial to improve the applicability and scalability of restoration techniques across different phytogeographical regions in our country.

Concluding Remarks

Several independent research groups have been studying biocrusts in Argentina, as evidenced by the increase in the number of studies since 2010 (Figure 1). However, many of these studies have limitations both in geographical and temporal scope. Research has primarily concentrated on one phytogeographical province (Monte), while other dryland phytogeographical provinces (Espinal, Chaco, Patagonia, Altos Andes, Puna, Prepuna and Subantarctic) received much less attention (Figure 2). The lack of long-term studies also limits our understanding of the temporal dynamics of biocrusts. Furthermore, the absence of coordinated efforts has resulted in a wide variety of measurement methods, complicating cross-study comparisons. Despite significant progress, much remains to be studied about the biology and ecology of biocrusts.

We need to improve the taxonomic classification of biocrust components in Argentina. Although numerous efforts have been made to identify biocrust taxa within the variety of biocrust structural types observed in the country (Figure 3), our knowledge is still limited. Given the bioclimatic and phytogeographic diversity of drylands in Argentina, biocrust biodiversity will exceed our current knowledge. Understanding biocrust distribution and species interactions requires overcoming all these taxonomic challenges. To do so, a close collaboration between ecologists and taxonomists, as well as the training of new taxonomists, is essential.

We need to quantify how biocrusts respond to multiple environmental factors. While significant research has investigated the effects of natural and anthropogenic factors on biocrust composition, abundance and functioning in Argentina, most studies have focused on a single factor. Research in other parts of the world shows that various drivers of biocrust structure and functioning interact with each other across spatial and temporal scales. Understanding how grazing interacts with increasing aridity, for example, is crucial for dryland conservation. Additionally, understanding the simultaneous effects of climatic and edaphic drivers on biocrusts is critical, mainly given the current context of climate and land use changes. Addressing the response of biocrusts to various stressors requires a coordinated effort, and consistent, homogeneous and systematic field protocols to produce comparable results.

Biocrusts are a valuable tool to restore degraded dryland soils, but efforts should focus on restoring the two-phase mosaic structure characteristic of dryland ecosystems and the essential functions provided by biocrusts and plants. Advances in biocrust restoration have focused primarily on developing techniques to grow biocrusts in greenhouses. However, to effectively restore degraded dryland soils, we must now focus on the transition from greenhouse to field reinoculation. The success of large-scale restoration projects in drylands will require reducing the gap between scientists and national agencies, such as The National Agricultural Technology Institute (INTA) and The National Parks Administration (APN).

Beyond their ecological role, biocrusts may offer significant economic benefits for sustainable development in Argentina. Their ability to enhance soil fertility through natural nitrogen fixation and improve soil stability can reduce reliance on synthetic fertilizers and erosion control actions, potentially lowering production costs in croplands. In grazing areas, preserving biocrusts can maintain pasture productivity, ensuring long-term economic viability. Additionally, restoration projects involving biocrusts can create local employment opportunities in rural areas, particularly where desertification is advancing. Incorporating biocrust conservation into land management strategies is not only an ecological necessity but also an economically strategic approach for promoting sustainable agricultural practices and rural development.

In summary, this review identifies several knowledge gaps in biocrust research in Argentina while also highlights significant progress made over the past two decades (Figure 4). With this review, we aim to establish a solid foundation for a more integrated and coordinated effort to deepen our understanding of biocrusts. As an emerging group of biocrust scientists, we have the expertise to implement this approach, but we want to incorporate new researchers from other disciplines to address as many aspects of biocrust biology and ecology as possible. Our immediate goal is to convene at the 2025 Argentinean Ecological Association Meeting (RAE 2025) to share ideas and foster collaborations, even with neighboring countries, where biocrust research is also in its early stages.

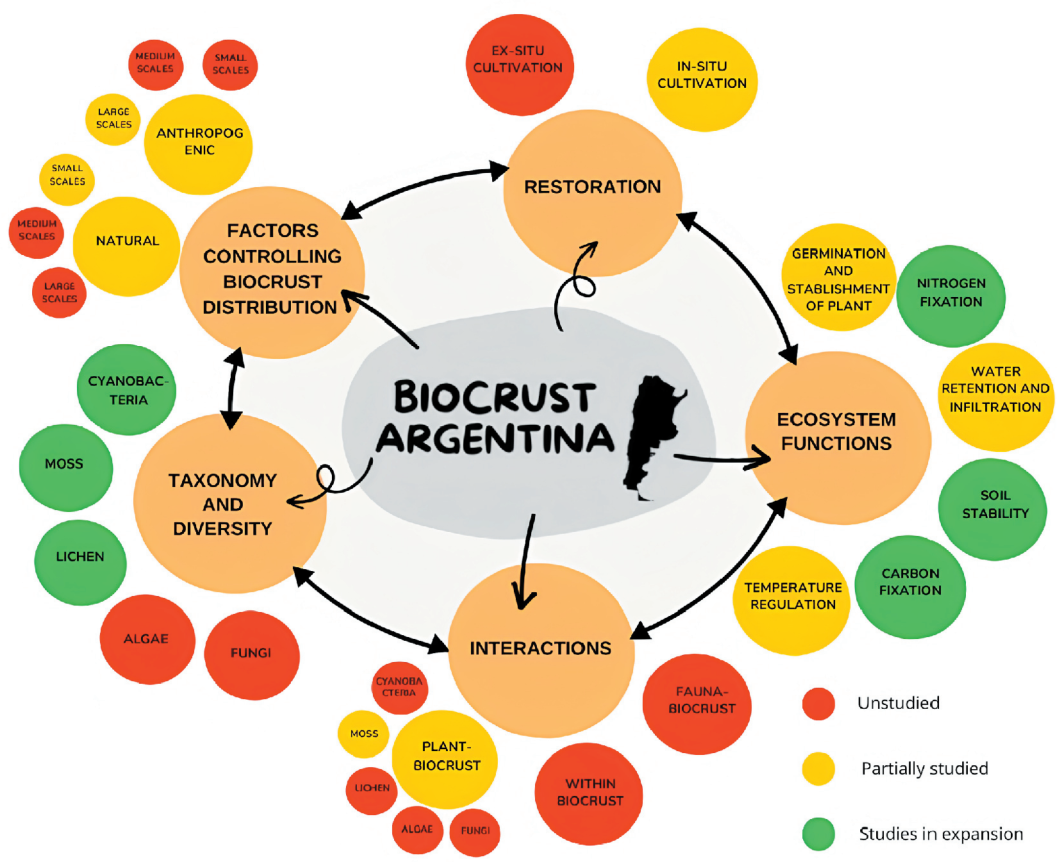

Figure 4. Schematic diagram showing the current extent of research on various topics related to biocrusts in Argentina (orange circles denote different topics in ecological studies on biocrusts).

Figura 4. Diagrama esquemático que muestra el alcance actual de la investigación sobre diversos temas relacionados con las biocostras en Argentina (los círculos naranjas muestran diferentes temas en estudios ecológicos sobre biocostras).

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