Annual Review of Microbiology

The Microbiology of Biological Soil Crusts

Ferran Garcia-Pichel

Center for Fundamental and Applied Microbiomics and School of Life Sciences, Arizona State University, Tempe, Arizona, USA; email: ferran@asu.edu

Annu. Rev. Microbiol. 2023. 77:149–71

The *Annual Review of Microbiology* is online at micro.annualreviews.org

https://doi.org/10.1146/annurev-micro-032521-015202

Keywords

arid lands, cyanobacteria, extreme environments, biogeochemistry, desiccation

Abstract

Biological soil crusts are thin, inconspicuous communities along the soil atmosphere ecotone that, until recently, were unrecognized by ecologists and even more so by microbiologists. In its broadest meaning, the term biological soil crust (or biocrust) encompasses a variety of communities that develop on soil surfaces and are powered by photosynthetic primary producers other than higher plants: cyanobacteria, microalgae, and cryptogams like lichens and mosses. Arid land biocrusts are the most studied, but biocrusts also exist in other settings where plant development is constrained. The minimal requirement is that light impinge directly on the soil; this is impeded by the accumulation of plant litter where plants abound. Since scientists started paying attention, much has been learned about their microbial communities, their composition, ecological extent, and biogeochemical roles, about how they alter the physical behavior of soils, and even how they inform an understanding of early life on land. This has opened new avenues for ecological restoration and agriculture.

Contents

1. INTRODUCTION

During the last few decades the study of biocrusts has increased exponentially (123), with several reviews and two ecological monographs dedicated to the subject (16, 19, 20, 47). All these contributions are recommended readings for the uninitiated. Nowadays biocrusts are considered one of the stable vegetation states of dryland regions (33) and have made it into soil microbiology textbooks (60). A review of their microbiology was, however, still missing. And yet microbes and microbial processes are a key part of biocrusts—often the totality of their biotic components. They deserve a much more detailed study than what can be achieved by treating biocrusts as black boxes embedded in larger ecological or edaphic systems.

Biocrusts are subject to extreme versions of the water-driven pulsed activity regime of arid land biota: Due to rapid evaporation, periods of hydration that support biological activity are short and transitions between hydrated and desiccated states are swift. The soil surface is also exposed to extremes of insolation, temperature, and erosional abrasion during long, inactive periods. This tough regime constrains which organisms inhabit biocrusts, how they evolve, and which functional processes they carry out and when. In this contribution I provide a critical review of what is known,

and what is not, regarding the microbiology of biocrusts and how microbes are key to understanding the biocrust clockwork, a necessary step to conserve and restore these small ecosystems of global consequence.

2. A PLURALITY OF BIOCRUSTS

While biocrusts are often treated as a unit, they encompass a marked, functionally relevant diversity of types. Sometimes they are virtually invisible, and sometimes only inconspicuous. They may follow the soil surface faithfully, display moderate levels of rugosity, or impose a decimeter-scale topographic relief to the soil surface. Soil texture and chemistry may also result in differentiated crusts, compositionally and structurally. But the most consequential distinction involves the type of primary producers: cyanobacterial (or microalgal), lichen, and moss crusts are the most important types. In terms of range in relative vertical scaling, the differences are tantamount to those found among grasslands and boreal forests, biomes hardly considered ecologically equivalent (**Figure 1**). Some basic properties are certainly shared among them: They all arm the soil surface effectively against erosion (54), modify soil surface albedo (42, 144), interact with soil hydrological properties (31, 46, 83), and increase soil organic carbon content (44), but they do differ in some key biological properties; some authors (34) have wisely warned that lumping all biocrusts together brings about a tangible risk of oversimplification.

2.1. Cyanocrusts

Cyanobacterial crusts (and microalgal biocrusts in some locales) are truly edaphic, forming an organo-sedimentary conglomerate within the soil proper whose physical integrity extends 0.5–1 cm deep. Initial colonization is carried out by motile, filamentous, nonheterocystous cyanobacteria that build bundles of filaments enclosed in a common extracellular exopolysaccharide sheath

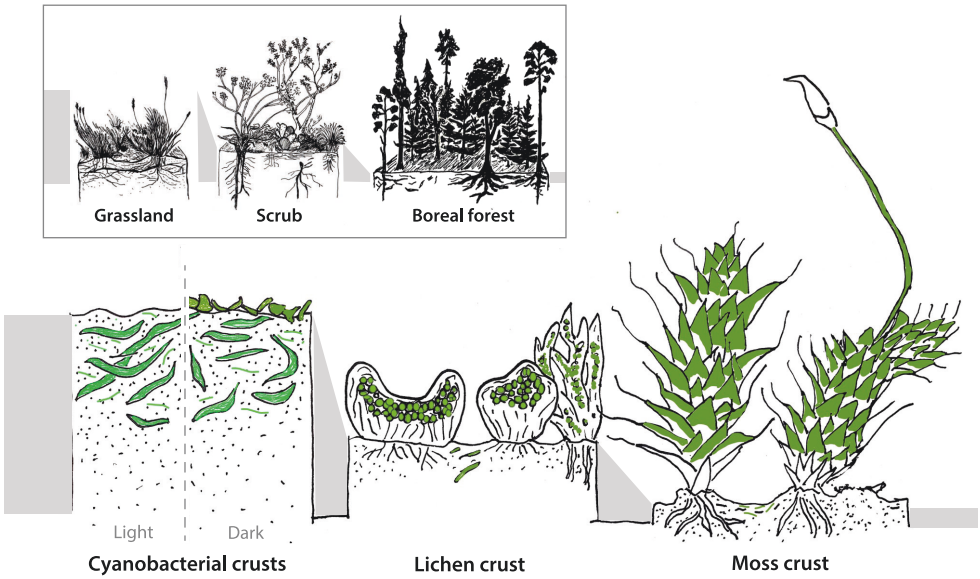

Figure 1

Vertical scales of biocrusts. (*Left* to *right*) Cyanobacterial (light and dark types), lichen, and moss crusts. Scales are progressively shrunk to accommodate their full extent. Green areas depict photosynthetic organisms or tissues. Inset shows different (macro)biomes that span similar relative differences.

and stabilize loose soil thanks to their self-aggregation and the weaving of mineral particles with exopolysaccharide trails (67). Once the crust is stabilized, other cyanobacteria will colonize it, typically nonmotile forms with dark sunscreen pigments. This more complex community is referred to as a dark cyanobacterial crust. When active, their in-soil photosynthesis relies simultaneously on CO_2 supplies from the atmosphere and soil stores. Activity is enabled by hydration from the soil solution and results in the formation of marked millimeter-sized microenvironments (58). Cyanobacterial biocrusts support significant aerobic hetero- and chemolithotrophic populations. Because many of the advances in knowledge of biocrust microbiology are based on cyanocrusts, it is unavoidable that this review will be biased in their favor.

2.2. Lichen Crusts

Lichen crusts are built by lichen thalli growing upward several millimeters into the air, held fast by rhizines that grow into the soil down to 1.5 cm (72), and quickly move soil water to the main thallus (36). Green algal lichen crusts dominate where water is mostly supplied as dew or fog (82). The photobionts within the lichen tissue (cyanobacteria or microalgae) are responsible for the bulk of primary productivity, drawing CO_2 from the air. Their photosynthate excretions are closely coupled to respiration and growth of the fungal partner (95), and likely also to the epiphytic and endophytic (11) bacterial communities they support. No direct determinations of the lichen leaching of organic carbon into the soil exist, though lichens certainly enrich bacterial populations and impart a distinct compositional character to the soil under their canopy (96, 104), perhaps through long-term decomposition of dead tissue (38).

2.3. Moss Crusts

Moss can tower centimeters above the soil when turgid, their photosynthetic leaflets being fully aerial and drawing atmospheric CO_2. Only rhizoids penetrate the soil. It is unknown whether mosses actively transport photosynthate to below-ground sinks like plants, but organics do demonstrably accumulate beneath them (146). Special morphological adaptations allow desert mosses to effectively gather atmospheric precipitation (112) in the face of their rudimentary water transport systems. They build the most effective type of crust in promoting soil water infiltration (32). Moss exposure to the elements likely contributes to their comparative environmental sensitivity to extremes. Mosses sustain associated epiphytic microbiomes that include many photo- and heterotrophic diazotrophs and cryoprotective bacteria (28, 117).

2.4. Successional Framework

Many parameters increase as one moves from cyanobacterial toward moss crusts, even in the same region or site, including areal chlorophyll *a* concentration (96), rates of photosynthesis and respiration (58, 149), amount of carbon leachates (79, 146), soil carbon and nitrogen pools (76), microbial population size and diversity (34, 96, 135), and complexity of co-occurring microbial networks (90). Some parameters decrease along the way, like the complexity of exudates in the soil or its N:C ratios (146). Yet others, like water infiltration, do not increase progressively (32), being minimal in lichen crusts. Many see in the differences outlined above a successional sequence, an attractive theoretical framework widely used to explain occurrence patterns and functional shifts. And yet, no single contribution has established directly a necessary and deterministic progression in time; space-for-time comparisons have always been used instead. The successional framework fails to account for the fact that moss crusts never develop in very arid locales. What may constitute a climax biocrust is rather constrained by local environmental factors related to aridity (57). It is true that in unconsolidated soils, only certain species of bundle-forming cyanobacteria are

pioneers, and that nonmotile cyanobacteria are secondary to the former. But in the subtropics, or in naturally stable soils, cyanobacterial populations of genera like *Nostoc* (109) and *Porphyrosiphon* (92) establish without prior or concurrent colonization by bundle-formers. Similarly, terrestrial lichens can be found on erosion-stable soils without a trace of cyanobacterial crusts around them.

3. EXTENT IN TIME AND SPACE

The current extent and distribution of biocrust can be gleaned not only from the innumerable reports of their presence in varied locales (19, 20) but also from quantitative approaches. Clearly, potential habitats are vast in that arid lands alone extend over 40% of the continents. Rough assessments based on geography and ground surveys are that biocrust cyanobacteria account for some 10^{14} g of carbon globally (61). Studies integrating local surveys with remote sensing show that cryptogamic covers (which also include other epilithic and epiphytic communities) account for some 7% of primary productivity and for nearly half of the biological nitrogen fixation on land (45). Despite uncertainties in these figures, biocrusts are undoubtedly relevant, global systems. Whatever they do matters for the big picture.

This extent must be understood as dynamic and dependent on climate. Looking into the past, stable isotope signatures preserved in Black Sea sediments reveal the starkly dynamic contribution of cyanobacterial biocrusts to central Asian steppes, in lockstep with shifting aridity, during the last 7,000 years (53). In the more recent past, over a timescale of centuries, vast expanses around centers highly populated by humans or areas of intense agriculture lost much of their crust cover because human activities have deleterious effects upon biocrusts, largely brought about by trampling by cattle, crop agriculture, and vehicular traffic. While these losses are patent, a quantitative retrospective has yet to be undertaken. Cyanocrusts are emerging as key modern analogs to understand early life on land before the advent of land plants during Earth's deep history. The notion that biocrusts represent the earliest form of extensive terrestrial ecosystems, capable of driving full-fledged global biogeochemical cycling and pedogenesis, is taking hold (134), supported by several lines of paleontological and phylogenetic evidence (21, 23).

Looking into the future, concerns that climate change may reduce their range and productivity at a fast pace are longstanding (48). Many studies have since provided evidence-based predictions. Future climate simulations in the field indeed invariably show reductions in cover of all types of crusts (49, 50, 93, 122) under warming or predicted shifts in precipitation patterns. Thermal and hydric niche breadth studies of biocrust species (64, 68, 150) speak for future alterations in species composition, distribution, and shifts in biogeochemical cycling processes (i.e., decrease of net nitrogen inputs). Models quantifying these effects at the global scale predict a dramatic shrinkage, by 25–40%, of biocrust cover within the next 65 years (125).

4. MICROBIOMES OF AN OPEN SYSTEM

4.1. Who Is There

Cyanocrusts sustain microbiomes containing in the order of 10^8–10^9 copies of 16S rRNA per square centimeter (15, 42, 106) in the top centimeter, most of which are attributable to bacteria. Archaea are a small proportion, around 5% (15, 130). Lichen crusts can reach somewhat higher concentrations (13). In both types, and contrary to the commonly held notion, nonlichenized fungi attain very low numbers, typically two to three orders of magnitude fewer than bacteria by ribosomal counts (12, 13, 15). Because fungi constitute the bulk of eukaryotic ribosomal gene counts in biocrust metagenomes (15), protists and animals must be rather rare as well. Metagenomic surveys show vanishingly few viruses in untreated biocrusts, though incubations of several days under

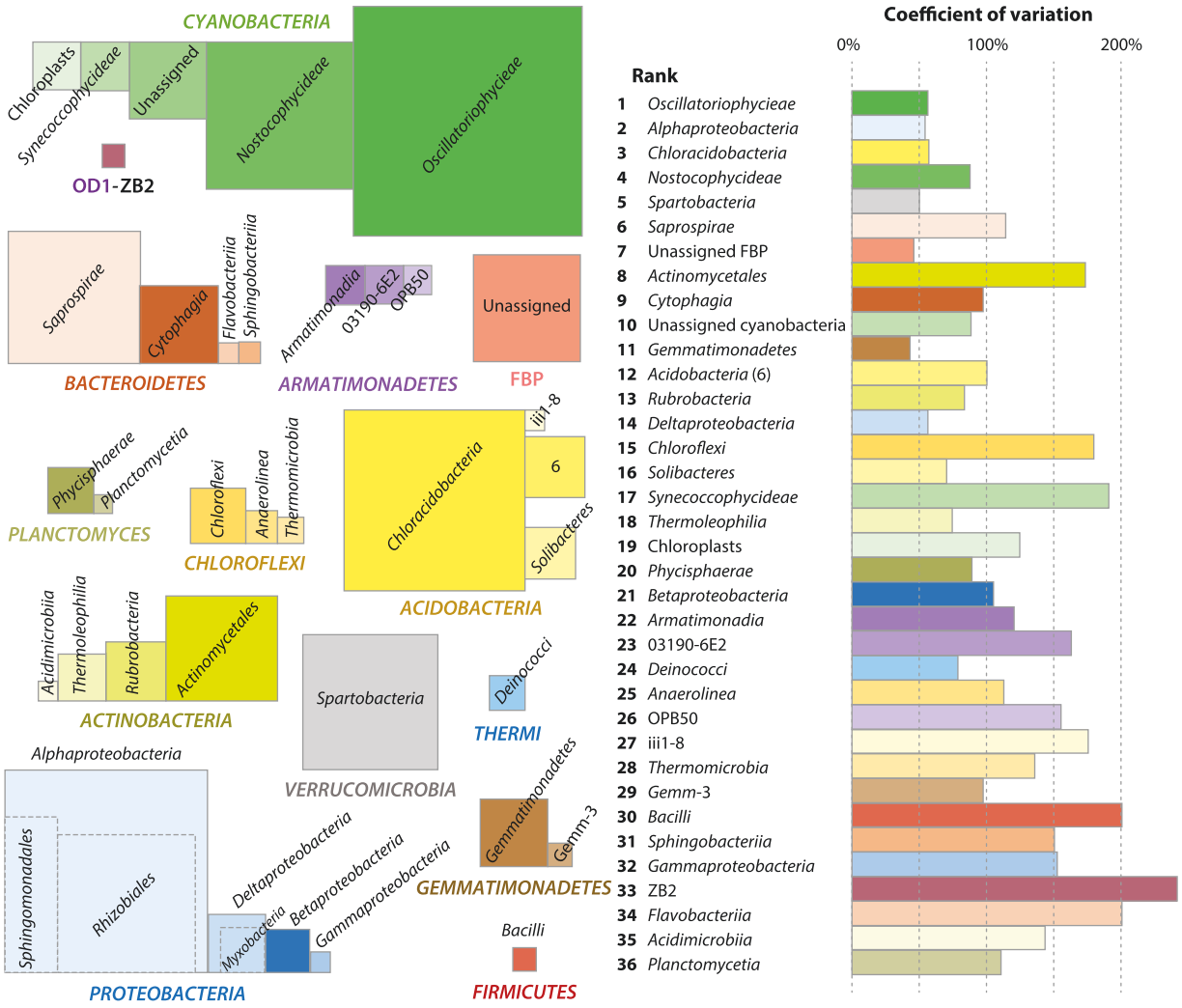

Figure 2

Typical composition of taxonomically assignable taxa in cyanocrust microbiomes (*left*) resolved to the class level and grouped by phylum using automated SILVA taxonomy, without an explicit endorsement of its nomenclatural validity, obtained by averaging 16S rRNA counts in 1-cm-deep biocrust samples from 20 sites across the Western United States. In addition to *Cyanobacteria*, *Alphaproteobacteria*, *Chloracidobacteria* (*Acidobacteria*), *Spartobacteria* (*Verrucomicrobia*), *Saprospirae*, and *Cytophagia* (*Bacteroidetes*), little-known members of candidate phylum FBP and several classes of *Actinobacteria* are commonly well represented. Some are more consistently common than others, as seen through coefficients of variation among sites (*right*). *Chloroflexi* are common but quite variable; *Bacilli* are often, but not always, rare.

hydration can elicit their proliferation (138). Consistently, virus-like particles could be retrieved only from crusts that had been incubated wet for several days (102).

Certain bacterial taxa beyond cyanobacteria are consistently abundant in biocrusts. **Figure 2** shows a compendium of surveys to provide a sense of what a typical cyanocrust microbiome may look like. Soil microbiomes of moss and lichen biocrusts differ somewhat from cyanobacterial microbiomes compositionally and in terms of functional gene classes (89, 101, 135, 136), although any functional consequences that might ensue from this divergence have not been determined.

Before one takes such generalizations too far, several caveats must be made. Firstly, horizontal variability is large, although no patterns of true endemism and no cases for true geographical restrictions to dispersal of biocrust organisms have been presented. Clear biogeographic patterns emerge recurrently within several continents (35, 64, 92), likely driven by local selection. The patterns can sometimes be traced to organismal physiological adaptations to temperature or rainfall frequency (51, 64, 68). Saline or gypsum-rich substrates impose distinctive signatures on composition through ionic stress (2, 63), as do more generally and less markedly other edaphic variations, even within neighboring crusts (103). Small-scale topography and proximity to plant canopies can also affect composition (25). Direct microbial interactions of mutualism (41), competition for space, and mutual segregation as well as bacterial predation (24) all matter at and below the centimeter scale.

Secondly, because biocrusts are fully open to the atmosphere, their composition may partly reflect allochthonous inputs. Bacterial deposition from the aerobiome can provide up to 10^8 16S rRNA gene copies cm^{-2} $month^{-1}$ during rainy seasons (143). Such inputs, aside from an overlooked source of organic carbon and nutrients, could contribute a compositional signal: A monsoon season's depositional load represents as many allochthonous bacteria as were in a typical cyanocrust already before it. Worse yet, deposition appears to be preferential for some taxa, like *Proteobacteria*, over others like *Actinobacteria* (143). Because the suspended arid land aerobiome tends to originate from unstable surfaces (52), it is probable that these bacterial inputs constitute a significant confounding factor.

Thirdly, the ribosomal methodology inherently underestimates microbes of large cell size (71). Cyanobacterial, algal, and fungal components may contribute more to relative biomass than one could surmise from size-biased molecular surveys, as comparisons of ribosomal and direct microscopy counts for fungi support (13).

Finally, because composition and biomass vary as one moves down and away from the influence of primary producers, comparisons should use a similar depth (commonly, and as used here, 1 cm). The deeper the sample, the more biocrusts will resemble the bulk soil microbiome; sampling 2 cm or deeper typically yields *Proteobacteria* or *Actinobacteria* instead of *Cyanobacteria* as the most abundant phylum, for example, or fails to detect metagenomic differences between crust types (15, 147).

4.2. Who Is Missing

Clearly, however, biocrusts exclude some microbial taxa or guilds that are typical of other photosynthetic microbial communities: Strict anaerobes like methanogens or acetogens and more oxygen-tolerant anoxygenic phototrophs, sulfate reducers, and spirochetes are all but absent. Temporary anaerobic microniches in wet crusts are apparently largely left to fermenters, possibly because of the fully oxic conditions reigning in intervening dry periods, much like in microbial mats from the upper intertidal zone, where the period between tidal floodings is inversely related to the relative contribution of obligate anaerobes (128). Consistently, much of a biocrust's diverse bacteria are culturable by aerobic plating (43), and many representative biocrust isolates have been fully described as novel taxa (14, 118–121).

4.3. Who Matters

Not only are there significant uncertainties in microbial tallies but there are important exceptions in biocrusts to the premise that abundant bacterial types are the most relevant. In spite of the high impact on biocrust nitrogen cycling, ammonia oxidizers are very rare [1 in 10^4 counts in **Figure 2**, 100-fold less by most-probable number (MPN) counts (78)], and ammonia-oxidizing archaea constitute less than 20 in 10^4 metagenomic ribosomal gene counts (15), consistent with *amoA* gene

counts (97). Their low numbers are incommensurate with their, very relevant, ammonia consumption. The obligatory predatory "*Candidatus* Cyanoraptor togatus" provides another example. It rarely exceeds 0.4% of ribosomal reads in healthy crusts, reaching only 4% in the full-fledged epidemics that nonetheless fully obliterate cyanobacterial communities (24). Unfortunately, surveys addressing the composition of the active fraction of biocrust microbiomes are so far unavailable.

4.4. Temporal Dynamics

While relevant studies are few, there are clear indications of a certain compositional seasonality (103, 109). It is also clear that microbiome composition responds to the frequency and duration of wet periods, a climatic parameter very variable in arid climates. Experimentally imposed severe drought swiftly promoted *Proteobacteria*, *Bacteroidetes*, and *Actinobacteria* over *Cyanobacteria* in absolute terms, and *Microcoleus vaginatus* over *Scytonema* spp. among major cyanobacteria (49). Conversely, varying precipitation event size (50), short pulses promoted cyanobacterial populations, and some taxa (*Parifilum*, *Scytonema*) over others (*M. vaginatus*). *Methylobacteriaceae*, *Geodermatophilaceae*, and *Micromonosporaceae* also benefited from shorter pulses. Further evidence comes from laboratory studies, where a few days under water-saturated conditions resulted in the demise of dominant cyanobacteria with the concomitant bloom to dominance of otherwise rare *Bacilli* (80) and the proliferation of their viruses (138). A few fully wet weeks can turn biocrusts into methanogenic communities (3). Thus, one can expect biocrust composition to be a complex trait, dependent on weather conditions antecedent to sampling.

5. ARCHITECTURE OF BIOCRUST MICROBIOMES

Most microbiomes assemble nonstochastically into reproducible patterns of spatial organization, or architecture, that constitute one of their emergent, defining traits. Biocrusts are no exception. Some architectural aspects of biocrusts have been resolved at microbially relevant scales, organization seemingly emerging as a result of two main drivers: organismal preference for microniches and interspecific microbial interactions.

5.1. Finding the Right Light

Light extinguishes quickly with depth, the photic zone (>1% of incident radiation) reaching no deeper than 1 mm or so, thus delimiting the presence of active phototrophs (**Figure 3**). But the actual light field, influenced by multiple scattering, causes somewhat unintuitive phenomena. The surface constitutes a light trap where the scalar irradiance can be much higher than the incident irradiance because it receives additional photons backscattered from below. The light field then progressively decays quasi-exponentially with depth, becoming increasingly more diffuse (less directional) in the process (56, 58, 62); these effects are much more pronounced in dry soils than in wet soils and are lessened by a preponderance of absorption over scattering (i.e., with increasing colonization level). Translucent pebbles or stable voids may increase light penetration significantly (115). Different cyanobacteria take advantage of these quirks. At the surface light trap we find sun-adapted sessile types (*Nostoc*, *Scytonema*, *Tolypothrix*) that invest heavily in sunscreens to survive very high levels of solar radiation during dry periods and contain low levels of photosynthetic pigments. The pioneer crust formers are all motile and shade adapted and are rich in photosynthetic pigments. They migrate in response to soil water availability between the surface, when wet, and a refugium some 0.2–0.6 mm below the surface, where they spend dry periods, thanks to their hydrotactic and phototactic abilities (65). The refugium provides sufficient illumination for photosynthesis when wet but shade during dry periods, minimizing exposure (**Figure 3**). Sometimes one finds a third, deep population that includes very low-light-adapted, nonmotile forms like

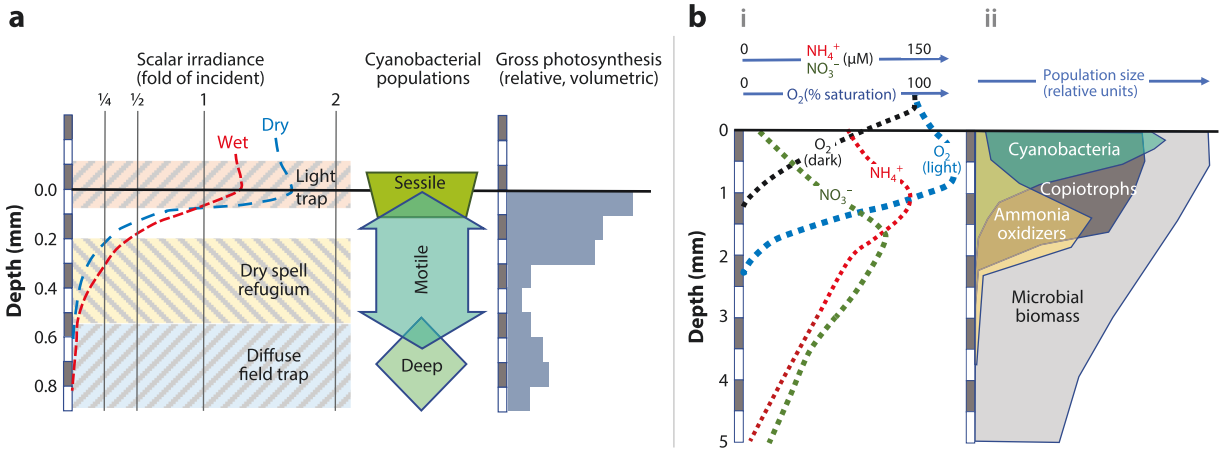

Figure 3

Typical architecture of cyanocrusts. (*a*) Patterns of vertical organization of photosynthetic populations and their activity in response to the light field. (*b*) Vertical distribution of selected bacterial types (*i*) and chemical microgradients ensuing from microbial activities (*ii*). Ammonia oxidizers were estimated with most-probable number (MPN) counts, cyanobacteria through chlorophyll *a*, copiotrophs with standard plating, and total biomass as extractable DNA. Data from References 56–59, 62, and 78.

Trichocoleus, *Pseudanabaena*, and chlorophyll *f*–containing (4) *Chroococcidiopsis*. It may also host part of the migrating populations that have lost their way in a completely diffuse light field where up and down cannot be discerned based merely on light directionality (diffusive light trap in **Figure 3**).

5.2. Finding the Right Fuel

Through the excretion or leaching of photosynthate, which is abundant and chemically diverse in biocrust cyanobacteria (7), a rich community of heterotrophs is supported, with evidence of heterotroph niche partitioning for specific metabolites (6). Heterotroph populations are orders of magnitude denser than those of bulk desert soils, numbers progressively dwindling with depth (62) as organics are utilized. Logically, one finds a progressive replacement with depth of copiotrophic heterotrophs by more oligotrophic types (62). An additional architectural segregation between copiotrophs and oligotrophs happens at yet smaller scales as a function of distance from bundles of cyanobacteria. Bundle-formers actively attract copiotrophic, diazotrophic heterotrophs while oligotrophs are relegated to the bulk (41, 108). Proximal heterotrophs enter in a carbon-for-nitrogen mutualistic exchange with the bundle-forming cyanobacteria that allows them to grow under nitrogen-limiting conditions (107). Ammonia oxidizers also show preferential distributions, with sharply delimited population peaks some 1.5–2 mm deep (78), at the bottom of the oxic zone (**Figure 3**), where abundant O_2 and ammonia are still available, but photoinhibition of ammonia monooxygenase (91) and competition for CO_2 with photoautotrophs (41) can be avoided.

6. TAKING A BIOCRUST'S PULSE: METABOLISM AND BIOGEOCHEMISTRY

Microbial metabolism and the ensuing biogeochemical processes are discontinuous in extent and character, driven by soil water content, and thus best understood when described along the sequence of a pulse of precipitation. During fully desiccated states, metabolism is principally halted, but it can start up swiftly. A few millimeters of rain suffice to saturate the crusted topsoil for some

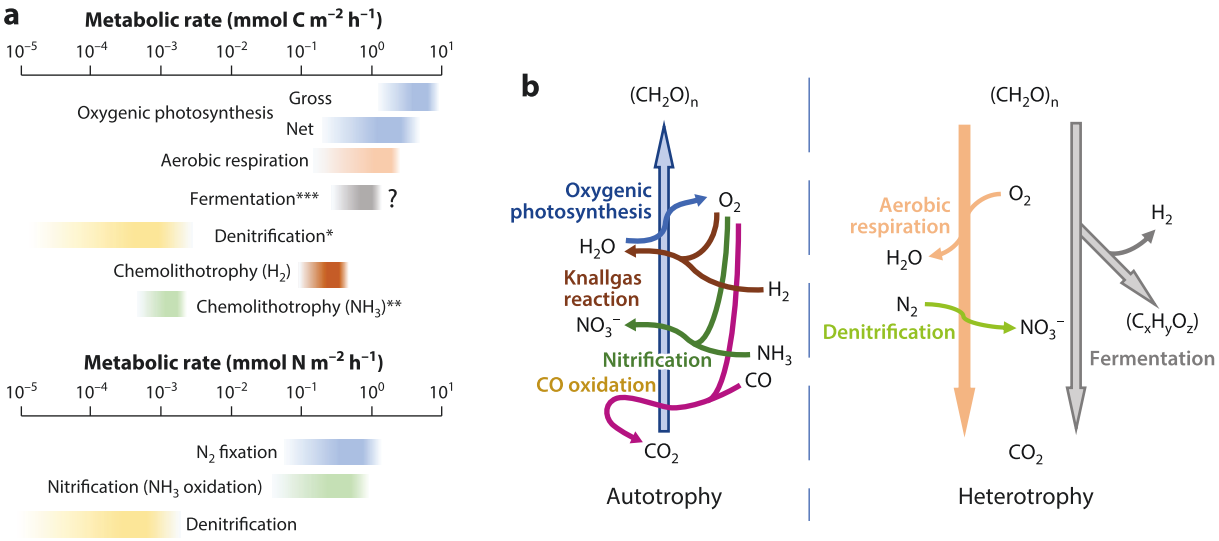

Figure 4

Major metabolism types and their instantaneous areal rate ranges for carbon and nitrogen in cyanobacterial crusts under water saturation. Typical ranges of process rates are in panel *a*. A schematic representation of biogeochemical transformations associated with specific microbial metabolism is in panel *b*. One asterisk indicates derivation from C/N stoichiometry for reduction of sugars to N_2. Two asterisks indicate derivation from reductant oxidation rates and typical growth yield coefficient. Three asterisks indicate an estimate based on H_2 supply needed for Knallgas reaction, and typical H_2/C yields. Data compiled from References 9, 15, 58, 78, 79, and 132.

time. Most early studies were conducted under soil saturation, but more recently, attention has been paid to the ensuing period of progressive soil desiccation.

6.1. Under Water Saturation

In the light, the major type of carbon metabolism is oxygenic photosynthesis, with depth-integrated gross rates in the order of 4–9 mmol O_2 (or C) m^{-2} h^{-1} (**Figure 4**), of which about half is internally respired and half constitutes the net photosynthesis or net primary productivity of the system (58). Net productivity, measured as O_2 export upward or import of CO_2 from above in cyanobacterial crusts, consistently hovers around 1–5 mmol O_2 (or C) m^{-2} h^{-1} (24, 58, 78, 116, 132). Second in importance is aerobic respiration (usually assessed as net O_2 consumption or CO_2 release in the dark), with rates equivalent to 20–70% of net productivity (58, 78, 116, 132), though aerobic respiration can be enhanced in the light because of internal oxygenation by photosynthesis (**Figure 4**). Oxygenic photosynthesis, concentrated in the photic zone, results in O_2 supersaturation close to the surface, as in other photosynthetic biofilms. Even in the light, aerobic respiration is demonstrably limited by diffusional O_2 transport, resulting in the formation of anoxic zones a few millimeters below the surface, in the aphotic zone. In darkness, O_2 penetrates less than 1 mm (**Figure 3**). Thus, the bulk of the crust is anoxic when water-saturated. Paradoxically, anaerobic respiration, including denitrification, does not ensue to any significant extent (9, 26, 79, 132), in the overwhelming majority of cases accounting for less than 0.1% of aerobic respiration in terms of carbon respired (**Figure 3**), unless long-term incubations under wetness are imposed (100). The lack of curvature in the NO_3^- profiles in the anoxic zone (**Figure 3**) indicates that nitrate is not actively consumed but merely diffuses downward. This leaves fermentation as the major potential type of carbon metabolism in the anoxic zones. Regrettably, fermentation rates have not been directly assessed.

Chemolithotrophy is important, including aerobic ammonia oxidation (78, 84), which is a proxy for full denitrification, aerobic H_2 oxidation (Knallgas reaction), and likely also aerobic CO oxidation (15, 98), but their respective anaerobic counterparts are either undetectable [anaerobic ammonium oxidation (ANAMMOX) (1, 132)] or unreported. Chemolithotrophy is thus likely relegated to oxic or microoxic layers. Hydrogenotrophic activity is attributable to various classes in the phylum *Actinobacteria*, and their potential rates of autotrophy can reach up to 10% of those attained by photoautotrophy (15); this translates to some 0.5 mmol C m^{-2} h^{-1} and is thus likely to contribute significantly to the fluxes of atmospheric CO_2 drawdown (net productivity) normally assigned to net photosynthesis, and even more so to the O_2 fluxes typically assigned to aerobic respiration. With a molar growth yield coefficient of 0.08 C per H_2 for Knallgas bacteria, the rates convert to around 6 mmol H_2 m^{-2} h^{-1}. Atmospheric H_2 being five orders of magnitude rarer than O_2, diffusional H_2 supplies could not possibly support such high rates, and a local source of H_2 must be present. It is logical to postulate that fermentative H_2 is at play, as is the case in functionally similar cyanobacterial mats from intertidal settings (74). To supply this H_2 through fermentation, in the absence of potentially competing H_2-dependent anaerobes, fermentation rates would have to be in the same order of magnitude as those of aerobic respiration. Fermentation is clearly a missing link in biocrust carbon cycling research. The contribution of denitrifiers to autotrophy based on ammonia oxidation rates is likely much smaller (less than 0.1% of photoautotrophy) because of its low molar yield coefficient [conservatively, 0.05 C per N (70)]. While rates of CO oxidation remain to be assessed, the CO oxygenase pathway is patent in several metagenomic biocrust surveys (15, 89, 135). Unlike most other soils (77), arid soils are a source of CO when dry, but not when wet (39), indicating moisture-driven consumption.

With respect to nitrogen metabolism, diazotrophy is prevalent, sustained, and virtually universal in biocrusts (10), a sure indicator that at least part of the microbiome functions under nitrogen limitation of growth. It is attributable to heterocystous cyanobacteria in dark cyanocrusts, cyanolichen crusts (145), and moss crusts (28), and to mutualistic heterotrophic diazotrophs in light cyanobacterial crusts (107, 113). While most determinations have been conducted using the acetylene reduction assay, with its associated uncertainties, typical instantaneous rates in the light are in the range of 20–200 μmol C_2H_4 m^{-2} s^{-1} (10, 78, 132, 150). Using an average biocrust-specific C_2H_2 -to-N_2 conversion ratio of 1.7 (75, 81, 131), this means some 70–700 μmol N m^{-2} s^{-1}. A large proportion of diazotrophic inputs is consistently subject to nitrification (78, 132), by both archaeal and bacterial ammonia oxidizers (97), likely after cell leakage and ammonification. Actual nitrification in situ is limited by oxygen, not ammonia (78). Denitrification rates, by contrast, are rather low (between 0.01 and 1 μmol N m^{-2} s^{-1}) (9, 26, 79, 132). Ammonia and nitrate thus accumulate in the pore space and are eventually exported with water percolation or runoff (79, 109, 133, 146); together with organic nitrogen, this constitutes the basis of the soil-fertilizing effect of biocrusts, keeping the biocrusts themselves in permanent need of new diazotrophic inputs. Gaseous nitrogen losses through ammonia volatilization and loss of partly oxidized nitrogenous gases are rather minor under water-saturated conditions (10), accounting for less than a few percentage points of inputs by fixation. Many of the distributional, metabolic, and biogeochemical traits of biocrusts under water saturation discussed here can be reproduced in silico through spatially explicit modeling that combines physicochemical and microbiological constraints (85).

6.2. Under Progressive Desiccation

The metabolic picture described above changes significantly when evaporation starts depleting soil water, increasing diffusivity of gases. This relieves diffusional limitations to major processes discussed above. Clearly delimited oxic/anoxic microniches fall apart, the overall level of oxygenation increases, solutes are concentrated in small water pockets whose pH shifts as salts precipitate

and equilibria reorganize in space (73, 86). Enhanced gas exchanges will principally ameliorate CO_2 limitation of photosynthesis, promote aerobic respiration over fermentation, depress internal fermentative H_2 production and thus the Knallgas reaction, and enhance ammonia oxidation. These predictions remain to be tested. But the most telltale, experimentally demonstrated shift has to do with the escape of intermediary gases of redox nitrogen transformations (mostly NO and HONO) as the soil dries, combined outgassing rates peaking slightly above 40 μmol N m^{-2} h^{-1} (142). Scaling up of such losses points to biocrusts as major sources of NO and HONO to the atmosphere globally (142). If the outgassing indeed stems from nitrification, as originally suggested, most or at least a large proportion of it must escape to the atmosphere at the peak of HO/HONO production, although we do not know whether nitrification itself, O_2-limited at water saturation, is concurrently enhanced or by how much. Further attempts to clarify the mechanism point to a desiccation-induced imbalance that causes accumulation of NO_2^- and NO_3^- in the pore space (94), inconsistent with a nitrification source. The ultimate cause remains unclear, as rates of denitrification or nitrification have not been measured during desiccation. Notably, however, mechanistic biotic/abiotic models can faithfully predict the experimental results without calling for unknown microbial transformations (86).

6.3. Integrating Activity Modes

Biogeochemically speaking, the metabolic shift between saturation and desiccation may translate into a switch of the role of biocrust from "mantles of fertility" (62, p. 312) to increasingly "futile cyclers," where much of the fixed N_2 returns to the atmosphere during progressive desiccation. It behooves us to elucidate whether and how such desiccation dynamics affect the other important biogeochemical transformations in biocrusts. Importantly, a full picture of net biocrust fluxes will not emerge until we understand processes under both conditions. Combined net effects will depend on the duration of pulses, the relative duration of fully saturated conditions being longer for more copious rain events.

6.4. A Role for Sophisticated Metabolites

Secondary metabolism seems to play a significant role in the biology of biocrust microbiomes. In addition to the sunscreen compounds synthesized by several biocrust microbes, active exometabolites that are yet to be identified play a demonstrable role in microbial interactions (108). The role of cyanobacterial toxins, so common in freshwater systems, is still unclear. Toxins like β-*N*-methylamino-l-alanine, 2,4-diaminobutyric acid, and N-(2-aminoethyl)glycine have been detected directly (99). Recent studies using long-read sequencing (137) highlight the rich genetic potential for secondary metabolites in these communities, demonstrating their differential transcription dynamics during wetting pulses. Siderophores and putative quorum-sensing signaling compounds are common, and nonribosomal peptides of uncertain role were extremely common. These studies point to an unexplored area in need of much more focused research.

7. ADAPTATIONS: TOWARD A NATURAL HISTORY OF BIOCRUST MICROBES

Biocrusts inhabit a unique environment at the interface between soils and atmosphere that constrains resource availability on the one hand and is subject to multiple stressors on the other, a tough combination that has left its imprint on biocrust organisms. Water, supplied in infrequent, short-lived events of precipitation or dew, is doubtless the major limiting resource to microbial activity. Biocrust organisms spend most of the time in a dehydrated, inactive state, accumulating environmental insults, which certainly demands a significant capacity to survive desiccation. At

the same time, they must be ready to quickly resume activity upon hydration to take advantage of short activity windows. This dual requirement constitutes a major determinant of community assembly, and translates into a requirement for anticipatory, integrative coordination between the system-wide states of quiescence and active growth that must take place rapidly at the physiological and genetic levels. Indeed, direct measurements show that metabolic resuscitation upon wetting is swift: A lag period for respiration usually cannot be detected, net photosynthesis can be measured within minutes (59), and nitrogen fixation starts within tens of minutes after wetting (58). The gene expression dynamics during such transitions has been revealed in the case of *M. vaginatus*, showing its complexity, the importance of early DNA damage repair, and the anticipatory gathering of reserve polymers before full desiccation (98). Appropriate transcripts useful during reactivation on rewetting are readied and stabilized shortly before desiccation in biocrust *Leptolyngbya* (111). And yet, many of the genes transcriptionally responsive to desiccation and rewetting are of unknown function (98, 111), so much remains to be learned.

7.1. NIRs Versus TORs

Successful biocrust microbes seem to adapt to the pulsed nature of their environment itself, rather than to either the active or inactive phases in it. On theoretical grounds this can be achieved by maintaining a constitutive capacity to fuel transitions in and out of dormancy (partly through a continual gathering of reserve polymers), which comes at the cost of a diminished growth potential (66). Successful biocrust inhabitants tend to be so-called NIR types (nimble responders; tough, but slow-growing) (66). Part of the space-time variability in community composition seen in biocrusts hinges on the differential capacity of specific organisms to adapt to varyingly pulsed regimes (50). Spore-forming microbes, like bacilli, many fungi, and some actinobacteria, while clearly desiccation resistant, are rather torpid responders (TORs) (66). Their sporulation and germination are complex and lengthy; thus, they are rare in biocrust plate counts (62), molecular surveys, and metagenomic analyses (98). None of the cyanobacteria that inhabit biocrusts produce akinetes (cyanobacterial spores) either. But unusually long periods of water availability can easily bring about a boon for fast-growing TORs, releasing communities from the NIR-type advantage imposed by the strongly pulsed regime. In this framework, biocrust organisms are typically more NIR than those in bulk soils, and biocrusts experiencing shorter pulses will select for organisms with a yet stronger NIR character. Extreme aridity with very short pulses eventually overwhelms the NIR strategy, as is the case of the central Atacama, central Namib, and Altar Deserts, where biocrusts are very rare.

7.2. Preemptive Adaptations

A general review of known bacterial adaptations to xeric conditions has been recently presented (88). Many of these are also adaptations to other stressors, and logically they apply to biocrust microbes as well. However, I focus here on those that appear specific to the habitat. Some have to do with the ability to effectively repair DNA damage accumulated during quiescence (98, 116). Some have to do with preventively diminishing the environmental damage incurred during quiescent periods, as is the case in the production of sunscreen compounds like scytonemin by heterocystous cyanobacteria and some of the cyanobacterial lichens (27). This single compound is accumulated to such a degree that it imparts the dark coloration in dark crusts. Cyanobacteria in biocrusts can also accumulate mycosporine-like amino acid sunscreens (55). Melanin-type sunscreens are produced by some biocrust actinobacteria (121) and dihydroxy-naphthalene melanins by ascomycetes (55). Whereas the synthesis of sunscreens is accomplished during periods of active growth, their main contribution to fitness takes place during metabolic dormancy, when active repair cannot

occur. The preemptive decoupling of light-harvesting systems from reaction centers in phototrophs is another example of a damage prevention strategy that will decrease photooxidative damage during quiescent periods (5), as does the migration toward environmental refugia below the surface in anticipation of desiccation by filamentous, nonheterocystous cyanobacteria (114). A strain of *Nostoc* is known to combine motility responses with sunscreen production in a bet-hedging strategy differentiated at the single-filament level (87) to maximize survival. Yet some adaptations are geared toward stabilizing cellular contents and osmotic forces as water becomes scarce, like the synthesis of compatible solutes during increasing water deficit (88), or the accumulation of antioxidants. The accumulation of compatible solutes during desiccation ameliorates the effects of cellular water loss and is a widespread capacity in biocrust organisms. Many of these osmolytes are lost to the cells during rehydration, becoming a major component of the biocrust exometabolome (6, 146).

7.3. Keeping Water Close

The synthesis of exopolysaccharides is very commonly called upon as an adaptation to desiccation in microbes (124). Exopolysaccharides are thought to slow the rate of water loss from cells, allowing for longer active periods and a more thorough physiological preparation for quiescence. This is demonstrably so in microbes that build macroscopic thalli, like *Nostoc commune* (129) and *M. vaginatus* (40). Generalized accumulation of diffusible polysaccharide within the biocrust pore space can bring benefits to all the inhabitants, as shown by the decrease in moisture-holding capacity brought about by degradation of exopolysaccharide during *Cyanoraptor* epidemics (24). Biocrust microbiomes have a stronger genetic potential to synthesize polysaccharides than those in adjacent bulk soil. The major contributors to this difference, judging from metagenomics, are *Alphaproteobacteria*, *Cyanobacteria*, *Chloroflexi*, and *Acidobacteria* (29); some biocrust isolates are slime hyperproducers, like the aptly named *Sphingomonas mucosissima* (118).

7.4. A Succulent Microbe?

A compilation of findings from several studies points to how the cyanobacterium *M. vaginatus* may coordinate several adaptive strategies to attain such a prominent role in biocrusts (**Figure 5**). It is

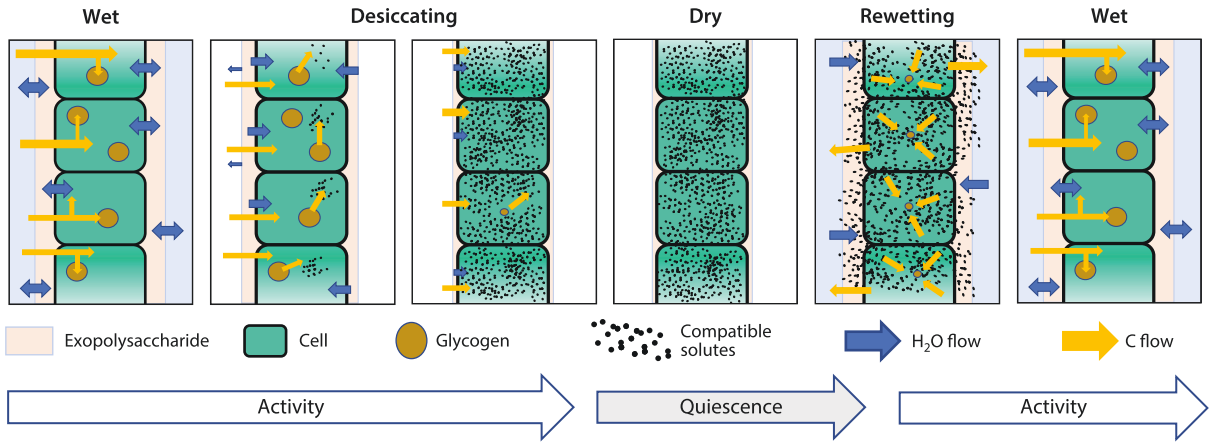

Figure 5

Model of integrated responses of compatible solutes (trehalose), exopolysaccharides, and glycogen reserves that may allow water retention and the effective extension of activity pulses in *Microcoleus vaginatus* (8, 40, 116).

one of the few species known to display hydrotaxis in anticipation of desiccation (114) to enhance survival during its inactive phase. Uniquely, and despite the fact that it ceases to photosynthesize at water potentials (Ψ) below just -3 MPa in cultures that do not build bundles, its field populations continue activity down to Ψ between -40 and -95 MPa (approximate water content of 1.5–0.5%). This indicates that it may possess a bundle-dependent means to "keep water potential higher in the immediate vicinity of the cells" (116, p. 2189). With this in mind, the desiccation dynamics of *M. vaginatus* bundles within the soil was studied using synchrotron X-ray tomography, demonstrating that the exopolysaccharide matrix shrinks through water loss to some 14% of the water-saturated volume as soil pore water content vanishes (40). But surprisingly, its cell volume increased concurrently by almost 60%, indicating that cells were not just slowing desiccation but also obtaining more water from their environment at the expense of water retained in the exopolysaccharide layers. A potential mechanism to accomplish this feat is the use of a unique, direct metabolic link between dihexose compatible solutes and glycogen reserves in *M. vaginatus* (8) that allows for fast turnover of their respective pools and enables it to respond swiftly to external downshifts in Ψ, rapidly drawing from an available carbon reserve rather than having to synthesize osmolytes de novo. Consistently, the onset of desiccation brings about increased expression of genes coding for glycogen-debranching enzymes (116). The rapid decrease in internal Ψ driven by swift conversion of glycogen into osmolytes could then be responsible for an osmotic influx of the water retained in the exopolysaccharide before it evaporates into the already dry soil pore space, possibly inching metabolic activity beyond what the soil Ψ would otherwise dictate. *M. vaginatus* seems to be the succulent among microbes.

8. BEYOND THE BIOCRUST BOUNDS

Interest in the microbial ecology of biocrusts has been undoubtedly spearheaded by a progressive realization of their impact on ecological processes, locally and globally. I only touch superficially on these so-called ecosystem services, since recent reviews are available (126). Biocrusts provide resistance to soil erosion by wind and water (18), effectively taking on this role precisely where plants cannot do so effectively because of their scarcity. In this way they become key agents in the sustainability of arid ecosystems. I briefly referenced above some of the microbial players and mechanisms involved in this trait. They are also regarded as "mantles of fertility," active importers of nutrients from the atmosphere into typically nutrient-poor arid ecosystems (62, p. 312). This involves carbon and nitrogen from gases, and phosphorous and metals from deposited aerosols (22).

The stabilizing and fertilizing effects of biocrusts on soil were soon seen as an opportunity to combat arid soil degradation, eliciting what is currently a multinational, exciting, and slowly progressing subdiscipline at the interface of microbiology and ecological restoration: developing biocrust nurseries to produce viable biocrust for inoculation on degraded soils (69, 127, 139, 148). Similarly, the fertilizing effects of biocrusts are opening an avenue to do away with constant chemical fertilization in agriculture (109, 110, 140). Dealing with unexpected difficulties in these applied developments of biocrust science has in turn contributed several fundamental advances in biocrust microbiology (24, 105, 107).

The possibility of more direct interactions between biocrusts and plants remains a matter of contention and does not lend itself easily to generalizations (73). In this respect, and because of its microbial basis, one must address the "fungal loop" hypothesis, which contends that fungal hyphae connect biocrusts to plant-root systems decimeters to meters apart, transporting nutrients from the crusts to the plants (37); it has gained some traction in arid land ecology. And yet, it lacks a microbiological foundation in that no fitness value to the fungi is apparent (or advanced) for that Herculean task. Cell-to-cell transport to reach 1 dm would require at least 10^5 mol ATP per mol

of nutrient molecule, and an alternative, passive diffusional transport would be exceedingly slow (one month for 1 dm and 1,500 years for 1 m). While a transfer of tracers between plants and crusts may occur in some instances (30), there is simply no evidence, conclusive or otherwise, for the agency of fungi in the process.

Another emergent consequence of biocrust cover has to do with warming the soil surface through modification of its albedo (42). In light of global warming trends, perhaps this effect should be called an ecosystem disservice. Finally, while there is general consensus that biocrusts alter the hydrological properties of surface soils, and that they can retain water within their bounds, the exact mechanisms and large-scale outcomes remain controversial, apparently dependent on soil properties, biocrust type, and even research team (17, 31, 83). One will have to await further clarification from the experts to settle this issue.

FUTURE ISSUES

1. The successional framework of biocrust development, at least for now, must be taken with caution, and would benefit from focused, direct interrogations to determine its applicability.
2. In the presence of significant uncertainties regarding the extent of exogenous microbes, relic DNA, and nonviable community members, we are in urgent need of biotic surveys that address and describe the active fraction of biocrust microbiomes.
3. The roles and consequences of fermentative metabolism in the carbon and hydrogen cycling of biocrusts needs to be investigated directly, as does the role and extent of CO metabolism.
4. The study of biogeochemistry within biocrusts must shift to address relevant processes concurrently, in an integrated fashion rather than focusing on single processes or rates, and include phenomenology during periods of water saturation and progressive desiccation.
5. To advance our understanding of microbial adaptations to the biocrust environment, genetically tractable model organisms need to be developed to enable direct interrogation by mutagenesis. Currently, none is available.
6. A consensus and complete view of the hydrological consequences of biocrusts must be arrived at, theoretically and experimentally, particularly given the great applied potential of biocrust horticulture for applications in conservation and agriculture.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

LITERATURE CITED

1. Abed RMM, Lam P, de Beer D, Stief P. 2013. High rates of denitrification and nitrous oxide emission in arid biological soil crusts from the Sultanate of Oman. *ISME J.* 7:1862–75
2. Abed RMM, Tamm A, Hassenrück C, Al-Rawahi AN, Rodríguez-Caballero E, et al. 2019. Habitat-dependent composition of bacterial and fungal communities in biological soil crusts from Oman. *Sci. Rep.* 9:6468

3. Angel R, Matthies D, Conrad R. 2011. Activation of methanogenesis in arid biological soil crusts despite the presence of oxygen. *PLOS ONE* 6:e20453
4. Antonaru LA, Cardona T, Larkum AWD, Nürnberg DJ. 2020. Global distribution of a chlorophyll *f* cyanobacterial marker. *ISME J.* 14:2275–87. Erratum. 2022. *ISME J.* 16:1680
5. Bar-Eyal L, Eisenberg I, Faust A, Raanan H, Nevo R, et al. 2015. An easily reversible structural change underlies mechanisms enabling desert crust cyanobacteria to survive desiccation. *Biochim. Biophys. Acta Bioenerget.* 1847:1267–73
6. Baran R, Brodie EL, Mayberry-Lewis J, Hummel E, da Rocha UN, et al. 2015. Exometabolite niche partitioning among sympatric soil bacteria. *Nat. Commun.* 6:8289
7. Baran R, Ivanova NN, Jose N, Garcia-Pichel F, Kyrpides NC, et al. 2013. Functional genomics of novel secondary metabolites from diverse cyanobacteria using untargeted metabolomics. *Mar. Drugs* 11:3617–31
8. Baran R, Lau R, Bowen BP, Diamond S, Jose N, et al. 2017. Extensive turnover of compatible solutes in cyanobacteria revealed by deuterium oxide (D_2O) stable isotope probing. *ACS Chem. Biol.* 12:674–81
9. Barger NN, Castle SC, Dean GN. 2013. Denitrification from nitrogen-fixing biologically crusted soils in a cool desert environment, southeast Utah, USA. *Ecol. Process.* 2:16
10. Barger NN, Weber B, Garcia-Pichel F, Zaady E, Belnap J. 2016. Patterns and controls on nitrogen cycling of biological soil crusts. See Ref. 141, pp. 257–85
11. Bates ST, Cropsey GW, Caporaso JG, Knight R, Fierer N. 2011. Bacterial communities associated with the lichen symbiosis. *Appl. Environ. Microbiol.* 77:1309–14
12. Bates ST, Garcia-Pichel F. 2009. A culture-independent study of free-living fungi in biological soil crusts of the Colorado Plateau: their diversity and relative contribution to microbial biomass. *Environ. Microbiol.* 11:56–67
13. Bates ST, Nash TH III, Sweat KG, Garcia-Pichel F. 2010. Fungal communities of lichen-dominated biological soil crusts: diversity, relative microbial biomass, and their relationship to disturbance and crust cover. *J. Arid Environ.* 74:1192–99
14. Bates ST, Reddy GS, Garcia-Pichel F. 2006. *Exophiala crusticola* anam. nov. (affinity *Herpotrichiellaceae*), a novel black yeast from biological soil crusts in the Western United States. *Int. J. Systemat. Evol. Microbiol.* 56:2697–702
15. Bay SK, Waite DW, Dong X, Gillor O, Chown SL, et al. 2021. Chemosynthetic and photosynthetic bacteria contribute differentially to primary production across a steep desert aridity gradient. *ISME J.* 15:3339–56
16. Belnap J. 2003. The world at your feet: desert biological soil crusts. *Front. Ecol. Environ.* 1:181–89
17. Belnap J. 2006. The potential roles of biological soil crusts in dryland hydrologic cycles. *Hydrol. Process. Int. J.* 20:3159–78
18. Belnap J, Büdel B. 2016. Biological soil crusts as soil stabilizers. See Ref. 141, pp. 305–20
19. Belnap J, Lange OL, eds. 2001. *Biological Soil Crusts: Structure, Function, and Management*. Berlin: Springer
20. Belnap J, Weber B, Büdel B. 2016. Biological soil crusts as an organizing principle in drylands. See Ref. 141, pp. 3–13
21. Beraldi-Campesi H, Farmer JD, Garcia-Pichel F. 2014. Modern terrestrial sedimentary biostructures and their fossil analogs in Mesoproterozoic subaerial deposits. *Palaios* 29:45–54
22. Beraldi-Campesi H, Hartnett H, Anbar A, Gordon G, Garcia-Pichel F. 2009. Effect of biological soil crusts on soil elemental concentrations: implications for biogeochemistry and as traceable biosignatures of ancient life on land. *Geobiology* 7:348–59
23. Beraldi-Campesi H, Retallack GJ. 2016. Terrestrial ecosystems in the Precambrian. See Ref. 141, pp. 37–54
24. Bethany J, Johnson SL, Garcia-Pichel F. 2022. High impact of bacterial predation on cyanobacteria in soil biocrusts. *Nat. Commun.* 13:4835
25. Bowker MA, Belnap J, Büdel B, Sannier C, Pietrasiak N, et al. 2016. Controls on distribution patterns of biological soil crusts at micro- to global scales. See Ref. 141, pp. 173–97
26. Brankatschk R, Fischer T, Veste M, Zeyer J. 2013. Succession of N cycling processes in biological soil crusts on a Central European inland dune. *FEMS Microbiol. Ecol.* 83:149–60

27. Büdel B, Karsten U, Garcia-Pichel F. 1997. Ultraviolet-absorbing scytonemin and mycosporine-like amino acid derivatives in exposed, rock-inhabiting cyanobacterial lichens. *Oecologia* 112:165–72
28. Calabria LM, Petersen KS, Bidwell A, Hamman ST. 2020. Moss-cyanobacteria associations as a novel source of biological N_2-fixation in temperate grasslands. *Plant Soil* 456:307–21
29. Cania B, Vestergaard G, Kublik S, Köhne JM, Fischer T, et al. 2020. Biological soil crusts from different soil substrates harbor distinct bacterial groups with the potential to produce exopolysaccharides and lipopolysaccharides. *Microb. Ecol.* 79:326–41
30. Carvajal Janke N, Coe KK. 2021. Evidence for a fungal loop in shrublands. *J. Ecol.* 109:1842–57
31. Chamizo S, Belnap J, Eldridge DJ, Cantón Y, Malam Issa O. 2016. The role of biocrusts in arid land hydrology. See Ref. 141, pp. 321–46
32. Chamizo S, Cantón Y, Lázaro R, Solé-Benet A, Domingo F. 2012. Crust composition and disturbance drive infiltration through biological soil crusts in semiarid ecosystems. *Ecosystems* 15:148–61
33. Chen N, Yu K, Jia R, Teng J, Zhao C. 2020. Biocrust as one of multiple stable states in global drylands. *Sci. Adv.* 6:eaay3763
34. Chilton AM, Neilan BA, Eldridge DJ. 2018. Biocrust morphology is linked to marked differences in microbial community composition. *Plant Soil* 429:65–75
35. Chilton AM, Nguyen STT, Nelson TM, Pearson LA, Neilan BA. 2022. Climate dictates microbial community composition and diversity in Australian biological soil crusts (biocrusts). *Environ. Microbiol.* 24:5467–82
36. Colesie C, Williams L, Büdel B. 2017. Water relations in the soil crust lichen *Psora decipiens* are optimized via anatomical variability. *Lichenologist* 49:483–92
37. Collins SL, Sinsabaugh RL, Crenshaw C, Green L, Porras-Alfaro A, et al. 2008. Pulse dynamics and microbial processes in aridland ecosystems. *J. Ecol.* 96:413–20
38. Concostrina-Zubiri L, Berdugo M, Valencia E, Mendoza BJ, Maestre FT. 2022. Decomposition of dryland biocrust-forming lichens and mosses contributes to soil nutrient cycling. *Plant Soil* 481:23–34
39. Conrad R, Seiler W. 1982. Arid soils as a source of atmospheric carbon monoxide. *Geophys. Res. Lett.* 9:1353–56
40. Couradeau E, Felde VJMNL, Parkinson D, Uteau D, Rochet A, et al. 2018. In situ X-ray tomography imaging of soil water and cyanobacteria from biological soil crusts undergoing desiccation. *Front. Environ. Sci.* 6:65
41. Couradeau E, Giraldo-Silva A, De Martini F, Garcia-Pichel F. 2019. Spatial segregation of the biological soil crust microbiome around its foundational cyanobacterium, *Microcoleus vaginatus*, and the formation of a nitrogen-fixing cyanosphere. *Microbiome* 7(1):55
42. Couradeau E, Karaoz U, Lim HC, da Rocha UN, Northen T, et al. 2016. Bacteria increase arid-land soil surface temperature through the production of sunscreens. *Nat. Commun.* 7:10373
43. da Rocha UN, Cadillo-Quiroz H, Karaoz U, Rajeev L, Klitgord N, et al. 2015. Isolation of a significant fraction of non-phototroph diversity from a desert biological soil crust. *Front. Microbiol.* 6:277
44. Dou W, Xiao B, Wang Y, Kidron GJ. 2022. Contributions of three types of biocrusts to soil carbon stock and annual efflux in a small watershed of Northern Chinese Loess Plateau. *Appl. Soil Ecol.* 179:104596
45. Elbert W, Weber B, Burrows S, Steinkamp J, Büdel B, et al. 2012. Contribution of cryptogamic covers to the global cycles of carbon and nitrogen. *Nat. Geosci.* 5:459–62
46. Eldridge DJ, Reed S, Travers SK, Bowker MA, Maestre FT, et al. 2020. The pervasive and multifaceted influence of biocrusts on water in the world's drylands. *Glob. Change Biol.* 26:6003–14
47. Evans R, Johansen J. 1999. Microbiotic crusts and ecosystem processes. *Crit. Rev. Plant Sci.* 18:183–225
48. Evans RD, Belnap J, Garcia-Pichel E, Phillips SL. 2001. Global change and the future of biological soil crusts. See Ref. 19, pp. 417–29
49. Fernandes VM, Machado de Lima NM, Roush D, Rudgers J, Collins SL, Garcia-Pichel F. 2018. Exposure to predicted precipitation patterns decreases population size and alters community structure of cyanobacteria in biological soil crusts from the Chihuahuan Desert. *Environ. Microbiol.* 20:259–69
50. Fernandes VM, Rudgers JA, Collins SL, Garcia-Pichel F. 2022. Rainfall pulse regime drives biomass and community composition in biological soil crusts. *Ecology* 103:e3744

51. Fernandes VMC, Giraldo-Silva A, Roush D, Garcia-Pichel F. 2021. Coleofasciculaceae, a monophyletic home for the *Microcoleus steenstrupii* complex and other desiccation-tolerant filamentous cyanobacteria. *J. Phycol.* 57:1563–79
52. Finn DR, Maldonado J, de Martini F, Yu J, Penton CR, et al. 2021. Agricultural practices drive biological loads, seasonal patterns and potential pathogens in the aerobiome of a mixed-land-use dryland. *Sci. Total Environ.* 798:149239
53. Fulton JM, Arthur MA, Freeman KH. 2012. Subboreal aridity and scytonemin in the Holocene Black Sea. *Org. Geochem.* 49:47–55
54. Gao L, Bowker MA, Xu M, Sun H, Tuo D, Zhao Y. 2017. Biological soil crusts decrease erodibility by modifying inherent soil properties on the Loess Plateau, China. *Soil Biol. Biochem.* 105:49–58
55. Gao Q, Garcia-Pichel F. 2011. Microbial ultraviolet sunscreens. *Nat. Rev. Microbiol.* 9:791–802
56. Garcia-Pichel F. 1995. A scalar irradiance fiber-optic microprobe for the measurement of ultraviolet radiation at high spatial resolution. *Photochem. Photobiol.* 61:248–54
57. Garcia-Pichel F. 2003. Desert environments: biological soil crusts. In *Encyclopedia of Environmental Microbiology*, ed. G Bitton, pp. 1019–23. New York: Wiley
58. Garcia-Pichel F, Belnap J. 1996. Microenvironments and microscale productivity of cyanobacterial desert crusts. *J. Phycol.* 32:774–82
59. Garcia-Pichel F, Belnap J. 2001. Small-scale environments and distribution of biological soil crusts. See Ref. 19, pp. 193–201
60. Garcia-Pichel F, Belnap J. 2021. Cyanobacteria and algae. In *Principles and Applications of Soil Microbiology*, ed. TJ Gentry, JJ Fuhrmann, DA Zuberer, pp. 171–89. Amsterdam: Elsevier. 3rd ed.
61. Garcia-Pichel F, Belnap J, Neuer S, Schanz F. 2003. Estimates of global cyanobacterial biomass and its distribution. *Arch. Hydrobiol Suppl. Algol. Stud.* 109:213–27
62. Garcia-Pichel F, Johnson S, Youngkin D, Belnap J. 2003. Small-scale vertical distribution of bacterial biomass and diversity in biological soil crusts from arid lands in the Colorado Plateau. *Microb. Ecol.* 46:312–21
63. Garcia-Pichel F, López-Cortés A, Nübel U. 2001. Phylogenetic and morphological diversity of cyanobacteria in soil desert crusts from the Colorado Plateau. *Appl. Environ. Microbiol.* 67:1902–10
64. Garcia-Pichel F, Loza V, Marusenko Y, Mateo P, Potrafka RM. 2013. Temperature drives the continental-scale distribution of key microbes in topsoil communities. *Science* 340:1574–77
65. Garcia-Pichel F, Pringault O. 2001. Cyanobacteria track water in desert soils. *Nature* 413:380–81
66. Garcia-Pichel F, Sala O. 2022. Expanding the pulse–reserve paradigm to microorganisms on the basis of differential reserve management strategies. *BioScience* 72:638–50
67. Garcia-Pichel F, Wojciechowski MF. 2009. The evolution of a capacity to build supra-cellular ropes enabled filamentous cyanobacteria to colonize highly erodible substrates. *PLOS ONE* 4:e7801
68. Giraldo-Silva A, Fernandes V, Bethany J, Garcia-Pichel F. 2020. Niche partitioning with temperature among heterocystous cyanobacteria (*Scytonema* spp., *Nostoc* spp., and *Tolypothrix* spp.) from biological soil crusts. *Microorganisms* 8:396
69. Giraldo-Silva A, Nelson C, Penfold C, Barger NN, Garcia-Pichel F. 2020. Effect of preconditioning to the soil environment on the performance of 20 cyanobacterial strains used as inoculum for biocrust restoration. *Restor. Ecol.* 28:S187–93
70. González-Cabaleiro R, Curtis TP, Ofiţeru ID. 2019. Bioenergetics analysis of ammonia-oxidizing bacteria and the estimation of their maximum growth yield. *Water Res.* 154:238–45
71. Gonzalez-de-Salceda L, Garcia-Pichel F. 2021. The allometry of cellular DNA and ribosomal gene content among microbes and its use for the assessment of microbiome community structure. *Microbiome* 9(1):173
72. Green TA, Pintado A, Raggio J, Sancho LG. 2018. The lifestyle of lichens in soil crusts. *Lichenologist* 50:397–410
73. Havrilla CA, Chaudhary VB, Ferrenberg S, Antoninka AJ, Belnap J, et al. 2019. Towards a predictive framework for biocrust mediation of plant performance: a meta-analysis. *J. Ecol.* 107:2789–807
74. Hoffmann D, Maldonado J, Wojciechowski MF, Garcia-Pichel F. 2015. Hydrogen export from intertidal cyanobacterial mats: sources, fluxes and the influence of community composition. *Environ. Microbiol.* 17:3738–53

75. Holst J, Butterbach-Bahl K, Liu C, Zheng X, Kaiser AJ, et al. 2009. Dinitrogen fixation by biological soil crusts in an Inner Mongolian steppe. *Biol. Fertility Soils* 45:679–90
76. Hu R, Wang X, Pan Y, Zhang Y, Zhang H, Chen N. 2015. Seasonal variation of net N mineralization under different biological soil crusts in Tengger Desert, North China. *CATENA* 127:9–16
77. Inman RE, Ingersoll RB, Levy EA. 1971. Soil: a natural sink for carbon monoxide. *Science* 172:1229–31
78. Johnson SL, Budinoff CR, Belnap J, Garcia-Pichel F. 2005. Relevance of ammonium oxidation within biological soil crust communities. *Environ. Microbiol.* 7:1–12
79. Johnson SL, Neuer S, Garcia-Pichel F. 2007. Export of nitrogenous compounds due to incomplete cycling within biological soil crusts of arid lands. *Environ. Microbiol.* 9:680–89
80. Karaoz U, Couradeau E, da Rocha UN, Lim H-C, Northen T, et al. 2018. Large blooms of Bacillales (Firmicutes) underlie the response to wetting of cyanobacterial biocrusts at various stages of maturity. *mBio* 9:e01366-16
81. Kasia C, Darwyn C, Paul S. 2013. Seasonal patterns of nitrogen fixation in biological soil crusts from British Columbia's Chilcotin grasslands. *Botany* 91:631–41
82. Kidron GJ, Kronenfeld R. 2022. Dew and fog as possible evolutionary drivers? The expansion of crustose and fruticose lichens in the Negev is respectively mainly dictated by dew and fog. *Planta* 255:32
83. Kidron GJ, Lichner L, Fischer T, Starinsky A, Or D. 2022. Mechanisms for biocrust-modulated runoff generation—a review. *Earth-Sci. Rev.* 231:104100
84. Kidron GJ, Posmanik R, Brunner T, Nejidat A. 2015. Spatial abundance of microbial nitrogen-transforming genes and inorganic nitrogen in biocrusts along a transect of an arid sand dune in the Negev Desert. *Soil Biol. Biochem.* 83:150–59
85. Kim M, Or D. 2017. Hydration status and diurnal trophic interactions shape microbial community function in desert biocrusts. *Biogeosciences* 14:5403–24
86. Kim M, Or D. 2019. Microscale pH variations during drying of soils and desert biocrusts affect HONO and NH_3 emissions. *Nat. Commun.* 10:3944
87. Klicki K, Ferreira D, Risser D, Garcia-Pichel F. 2022. A regulatory linkage between scytonemin production and hormogonia differentiation in *Nostoc punctiforme*. *iScience* 25:104361
88. Lebre PH, De Maayer P, Cowan DA. 2017. Xerotolerant bacteria: surviving through a dry spell. *Nat. Rev. Microbiol.* 15:285–96
89. Li J-Y, Jin X-Y, Zhang X-C, Chen L, Liu J-L, et al. 2020. Comparative metagenomics of two distinct biological soil crusts in the Tengger Desert, China. *Soil Biol. Biochem*. 140:107637
90. Li Y, Hu C. 2021. Biogeographical patterns and mechanisms of microbial community assembly that underlie successional biocrusts across northern China. *npj Biofilms Microbiomes* 7(1):15
91. Lu S, Liu X, Liu C, Cheng G, Shen H. 2020. Influence of photoinhibition on nitrification by ammonia-oxidizing microorganisms in aquatic ecosystems. *Rev. Environ. Sci. Bio/Technol.* 19:531–42
92. Machado-de-Lima NM, Fernandes VMC, Roush D, Velasco Ayuso S, Rigonato J, et al. 2019. The compositionally distinct cyanobacterial biocrusts from Brazilian savanna and their environmental drivers of community diversity. *Front. Microbiol.* 10:2798
93. Maestre FT, Escolar C, de Guevara ML, Quero JL, Lázaro R, et al. 2013. Changes in biocrust cover drive carbon cycle responses to climate change in drylands. *Glob. Change Biol.* 19:3835–47
94. Maier S, Kratz A, Weber J, Prass M, Liu F, et al. 2022. Water-driven microbial nitrogen transformations in biological soil crusts causing atmospheric nitrous acid and nitric oxide emissions. *ISME J.* 16:1012–24
95. Maier S, Schmidt TS, Zheng L, Peer T, Wagner V, Grube M. 2014. Analyses of dryland biological soil crusts highlight lichens as an important regulator of microbial communities. *Biodivers. Conserv.* 23:1735–55
96. Maier S, Tamm A, Wu D, Caesar J, Grube M, Weber B. 2018. Photoautotrophic organisms control microbial abundance, diversity, and physiology in different types of biological soil crusts. *ISME J.* 12:1032–46
97. Marusenko Y, Bates ST, Anderson I, Johnson SL, Soule T, Garcia-Pichel F. 2013. Ammonia-oxidizing archaea and bacteria are structured by geography in biological soil crusts across North American arid lands. *Ecol. Process.* 2:9

98. Meier DV, Imminger S, Gillor O, Woebken D, Lax S. 2021. Distribution of mixotrophy and desiccation survival mechanisms across microbial genomes in an arid biological soil crust community. *mSystems* 6:e00786-20
99. Metcalf JS, Banack SA, Richer R, Cox PA. 2015. Neurotoxic amino acids and their isomers in desert environments. *J. Arid Environ.* 112:140–44
100. Miralles I, Domingo F, García-Campos E, Trasar-Cepeda C, Leirós MC, Gil-Sotres F. 2012. Biological and microbial activity in biological soil crusts from the Tabernas desert, a sub-arid zone in SE Spain. *Soil Biol. Biochem.* 55:113–21
101. Moreira-Grez B, Tam K, Cross AT, Yong JW, Kumaresan D, et al. 2019. The bacterial microbiome associated with arid biocrusts and the biogeochemical influence of biocrusts upon the underlying soil. *Front. Microbiol.* 10:2143
102. Mugnai G, Stuknytė M, Arioli S, Gargari G, Adessi A, Mora D. 2021. Virus-like particles isolated from reactivated biological soil crusts. *Biol. Fertil. Soils* 57:863–68
103. Nagy ML, Pérez A, Garcia-Pichel F. 2005. The prokaryotic diversity of biological soil crusts in the Sonoran Desert (Organ Pipe Cactus National Monument, AZ). *FEMS Microbiol. Ecol.* 54:233–45
104. Navarro-Noya YE, Jiménez-Aguilar A, Valenzuela-Encinas C, Alcántara-Hernández RJ, Ruíz-Valdiviezo VM, et al. 2014. Bacterial communities in soil under moss and lichen-moss crusts. *Geomicrobiol. J.* 31:152–60
105. Nelson C, Garcia-Pichel F. 2021. Beneficial cyanosphere heterotrophs accelerate establishment of cyanobacterial biocrust. *Appl. Environ. Microbiol.* 87:e01236-21
106. Nelson C, Giraldo-Silva A, Garcia-Pichel F. 2020. A fog-irrigated soil substrate system unifies and optimizes cyanobacterial biocrust inoculum production. *Appl. Environ. Microbiol.* 86:e00624-20
107. Nelson C, Giraldo-Silva A, Garcia-Pichel F. 2021. A symbiotic nutrient exchange within the cyanosphere microbiome of the biocrust cyanobacterium, *Microcoleus vaginatus*. *ISME J.* 15:282–92
108. Nelson C, Giraldo-Silva A, Warsop Thomas F, Garcia-Pichel F. 2022. Spatial self-segregation of pioneer cyanobacterial species drives microbiome organization in biocrusts. *ISME Commun.* 2(1):114
109. Nevins CJ, Inglett PW, Reardon CL, Strauss SL. 2022. Seasonality drives microbiome composition and nitrogen cycling in soil below biocrusts. *Soil Biol. Biochem.* 166:108551
110. Nevins CJ, Inglett PW, Strauss SL. 2021. Biological soil crusts structure the subsurface microbiome in a sandy agroecosystem. *Plant Soil* 462:311–29
111. Oren N, Raanan H, Kedem I, Turjeman A, Bronstein M, et al. 2019. Desert cyanobacteria prepare in advance for dehydration and rewetting: the role of light and temperature sensing. *Mol. Ecol.* 28:2305–20
112. Pan Z, Pitt WG, Zhang Y, Wu N, Tao Y, Truscott TT. 2016. The upside-down water collection system of *Syntrichia caninervis*. *Nat. Plants* 2:16076
113. Pepe-Ranney C, Koechli C, Potrafka R, Andam C, Eggleston E, et al. 2016. Non-cyanobacterial diazotrophs mediate dinitrogen fixation in biological soil crusts during early crust formation. *ISME J.* 10:287–98
114. Pringault O, Garcia-Pichel F. 2004. Hydrotaxis of cyanobacteria in desert crusts. *Microb. Ecol.* 47:366–73
115. Raanan H, Felde VJMNL, Peth S, Drahorad S, Ionescu D, et al. 2016. Three-dimensional structure and cyanobacterial activity within a desert biological soil crust. *Environ. Microbiol.* 18:372–83
116. Rajeev L, da Rocha UN, Klitgord N, Luning EG, Fortney J, et al. 2013. Dynamic cyanobacterial response to hydration and dehydration in a desert biological soil crust. *ISME J.* 7:2178–91
117. Raymond JA. 2016. Dependence on epiphytic bacteria for freezing protection in an Antarctic moss, *Bryum argenteum*. *Environ. Microbiol. Rep.* 8:14–19
118. Reddy G, Garcia-Pichel F. 2007. *Sphingomonas mucosissima* sp. nov. and *Sphingomonas desiccabilis* sp. nov., from biological soil crusts in the Colorado Plateau, USA. *Int. J. Systemat. Evol. Microbiol.* 57:1028–34
119. Reddy GS, Garcia-Pichel F. 2009. Description of *Patulibacter americanus* sp. nov., isolated from biological soil crusts, emended description of the genus *Patulibacter* Takahashi et al. 2006 and proposal of *Solirubrobacterales* ord. nov. and *Thermoleophilales* ord. nov. *Int. J. Systemat. Evol. Microbiol.* 59:87–94
120. Reddy GS, Nagy M, Garcia-Pichel F. 2006. *Belnapia moabensis* gen. nov., sp. nov., an alphaproteobacterium from biological soil crusts in the Colorado Plateau, USA. *Int. J. Systemat. Evol. Microbiol.* 56:51–58

121. Reddy GS, Potrafka RM, Garcia-Pichel F. 2007. *Modestobacter versicolor* sp. nov., an actinobacterium from biological soil crusts that produces melanins under oligotrophy, with emended descriptions of the genus *Modestobacter* and *Modestobacter multiseptatus* Mevs et al. 2000. *Int. J. Systemat. Evol. Microbiol.* 57:2014–20
122. Reed SC, Coe KK, Sparks JP, Housman DC, Zelikova TJ, Belnap J. 2012. Changes to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nat. Climate Change* 2:752–55
123. Reed SC, Delgado-Baquerizo M, Ferrenberg S. 2019. Biocrust science and global change. *New Phytol.* 223:1047–51
124. Roberson EB, Firestone MK. 1992. Relationship between desiccation and exopolysaccharide production in a soil *Pseudomonas* sp. *Appl. Environ. Microbiol.* 58:1284–91
125. Rodriguez-Caballero E, Belnap J, Büdel B, Crutzen PJ, Andreae MO, et al. 2018. Dryland photoautotrophic soil surface communities endangered by global change. *Nat. Geosci.* 11:185–89
126. Rodríguez-Caballero E, Castro AJ, Chamizo S, Quintas-Soriano C, Garcia-Llorente M, et al. 2018. Ecosystem services provided by biocrusts: from ecosystem functions to social values. *J. Arid Environ.* 159:45–53
127. Román JR, Roncero-Ramos B, Chamizo S, Rodríguez-Caballero E, Cantón Y. 2018. Restoring soil functions by means of cyanobacteria inoculation: importance of soil conditions and species selection. *Land Degrad. Dev.* 29:3184–93
128. Rothrock MJ Jr., Garcia-Pichel F. 2005. Microbial diversity of benthic mats along a tidal desiccation gradient. *Environ. Microbiol.* 7:593–601
129. Scherer S, Zhong Z-P. 1991. Desiccation independence of terrestrial *Nostoc* commune ecotypes (cyanobacteria). *Microb. Ecol.* 22:271–83
130. Soule T, Anderson IJ, Johnson SL, Bates ST, Garcia-Pichel F. 2009. Archaeal populations in biological soil crusts from arid lands in North America. *Soil Biol. Biochem.* 41:2069–74
131. Stewart KJ, Coxson D, Grogan P. 2011. Nitrogen inputs by associative cyanobacteria across a low arctic tundra landscape. *Arct. Antarct. Alp. Res.* 43:267–78
132. Strauss SL, Day TA, Garcia-Pichel F. 2012. Nitrogen cycling in desert biological soil crusts across biogeographic regions in the Southwestern United States. *Biogeochemistry* 108:171–82
133. Thiet RK, Boerner REJ, Nagy M, Jardine R. 2005. The effect of biological soil crusts on throughput of rainwater and N into Lake Michigan sand dune soils. *Plant Soil* 278:235–51
134. Thomazo C, Couradeau E, Garcia-Pichel F. 2018. Possible nitrogen fertilization of the early Earth Ocean by microbial continental ecosystems. *Nat. Commun.* 9(1):2530
135. Tian C, Pang J, Bu C, Wu S, Li Y, et al. 2022. The microbiomes in lichen and moss biocrust contribute differently to carbon and nitrogen cycles in arid ecosystems. *Microb. Ecol.* In press. **https://doi.org/10.1007/s00248-022-02077-7**
136. Tian C, Xi J, Ju M, Li Y, Guo Q, et al. 2021. Biocrust microbiomes influence ecosystem structure and function in the Mu Us Sandland, northwest China. *Ecol. Informat.* 66:101441
137. Van Goethem MW, Osborn AR, Bowen BP, Andeer PF, Swenson TL, et al. 2021. Long-read metagenomics of soil communities reveals phylum-specific secondary metabolite dynamics. *Commun. Biol.* 4:1302
138. Van Goethem MW, Swenson TL, Trubl G, Roux S, Northen TR, Martiny JBH. 2019. Characteristics of wetting-induced bacteriophage blooms in biological soil crust. *mBio* 10:e02287-19
139. Velasco Ayuso S, Giraldo Silva A, Nelson C, Barger NN, Garcia-Pichel F. 2018. Microbial nursery production of high-quality biological soil crust biomass for restoration of degraded dryland soils. *Appl. Environ. Microbiol.* 83:e02179-16
140. Wang W, Wang B-Z, Zhou R, Ullah A, Zhao Z-Y, et al. 2022. Biocrusts as a nature-based strategy (NbS) improve soil carbon and nitrogen stocks and maize productivity in semiarid environment. *Agric. Water Manag.* 270:107742
141. Weber B, Büdel B, Belnap J, eds. 2016. *Biological Soil Crusts: An Organizing Principle in Drylands*. Cham, Switz.: Springer
142. Weber B, Wu D, Tamm A, Ruckteschler N, Rodríguez-Caballero E, et al. 2015. Biological soil crusts accelerate the nitrogen cycle through large NO and HONO emissions in drylands. *PNAS* 112:15384–89
143. Woo C, Yamamoto N. 2020. Falling bacterial communities from the atmosphere. *Environ. Microbiome* 15(1):22

144. Xiao B, Bowker MA. 2020. Moss-biocrusts strongly decrease soil surface albedo, altering land-surface energy balance in a dryland ecosystem. *Sci. Total Environ.* 741:140425
145. Yeager CM, Kornosky JL, Morgan RE, Cain EC, Garcia-Pichel F, et al. 2007. Three distinct clades of cultured heterocystous cyanobacteria constitute the dominant N_2-fixing members of biological soil crusts of the Colorado Plateau, USA. *FEMS Microbiol. Ecol.* 60:85–97
146. Young KE, Ferrenberg S, Reibold R, Reed SC, Swenson T, et al. 2022. Vertical movement of soluble carbon and nutrients from biocrusts to subsurface mineral soils. *Geoderma* 405:115495
147. Zhang B, Kong W, Wu N, Zhang Y. 2016. Bacterial diversity and community along the succession of biological soil crusts in the Gurbantunggut Desert, Northern China. *J. Basic Microbiol.* 56:670–79
148. Zhao Y, Bowker MA, Zhang Y, Zaady E. 2016. Enhanced recovery of biological soil crusts after disturbance. See Ref. 141, pp. 499–523
149. Zhao Y, Zhang Z, Hu Y, Chen Y. 2016. The seasonal and successional variations of carbon release from biological soil crust-covered soil. *J. Arid Environ.* 127:148–53
150. Zhou X, Smith H, Giraldo Silva A, Belnap J, Garcia-Pichel F. 2016. Differential responses of dinitrogen fixation, diazotrophic cyanobacteria and ammonia oxidation reveal a potential warming-induced imbalance of the N-cycle in biological soil crusts. *PLOS ONE* 11:e0164932