

In Living Color: Pigment-Based Microbial Ecology at the Mineral–Air Interface

FEDERICA VILLA[✉], YING-LI WU, ANDREA ZERBONI, AND FRANCESCA CAPPITELLI

Pigment-based color is one of the most important phenotypic traits of biofilms at the mineral–air interface (subaerial biofilms, SABs), because it reflects the physiology of the microbial community. Because color is the hallmark of all SABs, we argue that pigment-based color could convey the mechanisms that drive microbial adaptation and coexistence across different terrestrial environments and link phenotypic traits to community fitness and ecological dynamics. Within this framework, we present the most relevant microbial pigments at the mineral–air interface and discuss some of the evolutionary landscapes that necessitate pigments as adaptive strategies for resource allocation and survivability. We report several pigment features that reflect SAB communities' structure and function, as well as pigment ecology in the context of microbial life-history strategies and coexistence theory. Finally, we conclude the study of pigment-based ecology by presenting its potential application and some of the key challenges in the research.

Keywords: pigments, color, subaerial biofilm, mineral–air interface, pigment ecology

The mineral–air interface is a large and ancient ecological niche that exists on a wide range of scales from microscopic to planetary. Despite the stark environment, the mineral–air interface hosts a micron- to a millimeter-thick veneer of densely packed microorganisms that operate within self-organized structures called *subaerial biofilms* (SABs; Villa et al. 2016). Examples of SAB communities are those retrieved from mineral grain in the topsoil of hot and cold deserts (e.g., biocrusts), air-exposed rocks, and outdoor stone monuments. Given the oligotrophic nature of mineral substrates, the SABs are mainly supported by photosynthetic interactions, where chemoorganotrophic assemblages in this ecosystem are driven by phototrophic carbon fixation (Villa et al. 2016). Chemoorganotrophs, as it turns out, promote cyanobacterial growth by consuming oxygen, supplying key metabolites, and scavenging waste products (Villa and Cappitelli 2019). According to an estimate, the global photoautotrophic communities on terrestrial mineral surfaces contribute to approximately 7% of the net primary production by terrestrial vegetation and half of the biological nitrogen fixation on land (Elbert et al. 2012). This highlights the fundamental role of the mineral–SAB–air interactive system in the Earth critical zone—a thin veneer where physical, chemical, and biological processes interact to sustain life on our planet (Brantley et al. 2007, Richter and Mobley 2009).

Besides being a nutrient-poor habitat, the mineral–air interface often undergoes rapid changes in moisture, temperature, and irradiation level, all of which promote the development of specialized microorganisms with efficient metabolic stress responses (Gorbushina 2007). These sharp changes in the extracellular environment make SABs excellent ecosystem models for studying multiple survival strategies in terrestrial and extraterrestrial settings.

To assess the nature and function of these survival strategies, one of the most important elements is the SAB's color—an omnipresent phenotypic feature in the microbial communities at the mineral–air interface (figure 1). To generate colors, most SAB-dwelling cells rely on light-absorbing compounds called *pigments*. Up to now, microbial pigments have been largely investigated for industrial and medical applications (*inter alia* Ramesh et al. 2019, Kalra et al. 2020, Sajjad et al. 2020, Venil et al. 2020, Celedón and Díaz 2021, Chatragadda and Dufossé 2021). In addition, most studies on pigmented biofilms have been focused on aquatic environments instead of terrestrial ecosystems, neglecting the physiological and ecological role of color on the SABs.

Considering the aforementioned, we argue that pigment-based color could convey information about the mechanisms that drive microbial adaptation and coexistence across different environments and could possibly link phenotypic

BioScience 72: 1156–1175. © The Author(s) 2022. Published by Oxford University Press on behalf of the American Institute of Biological Sciences. This is an Open Access article distributed under the terms of the Creative Commons Attribution-NonCommercial License (<https://creativecommons.org/licenses/by-nc/4.0/>), which permits non-commercial re-use, distribution, and reproduction in any medium, provided the original work is properly cited. For commercial re-use, please contact journals.permissions@oup.com <https://doi.org/10.1093/biosci/biac091>

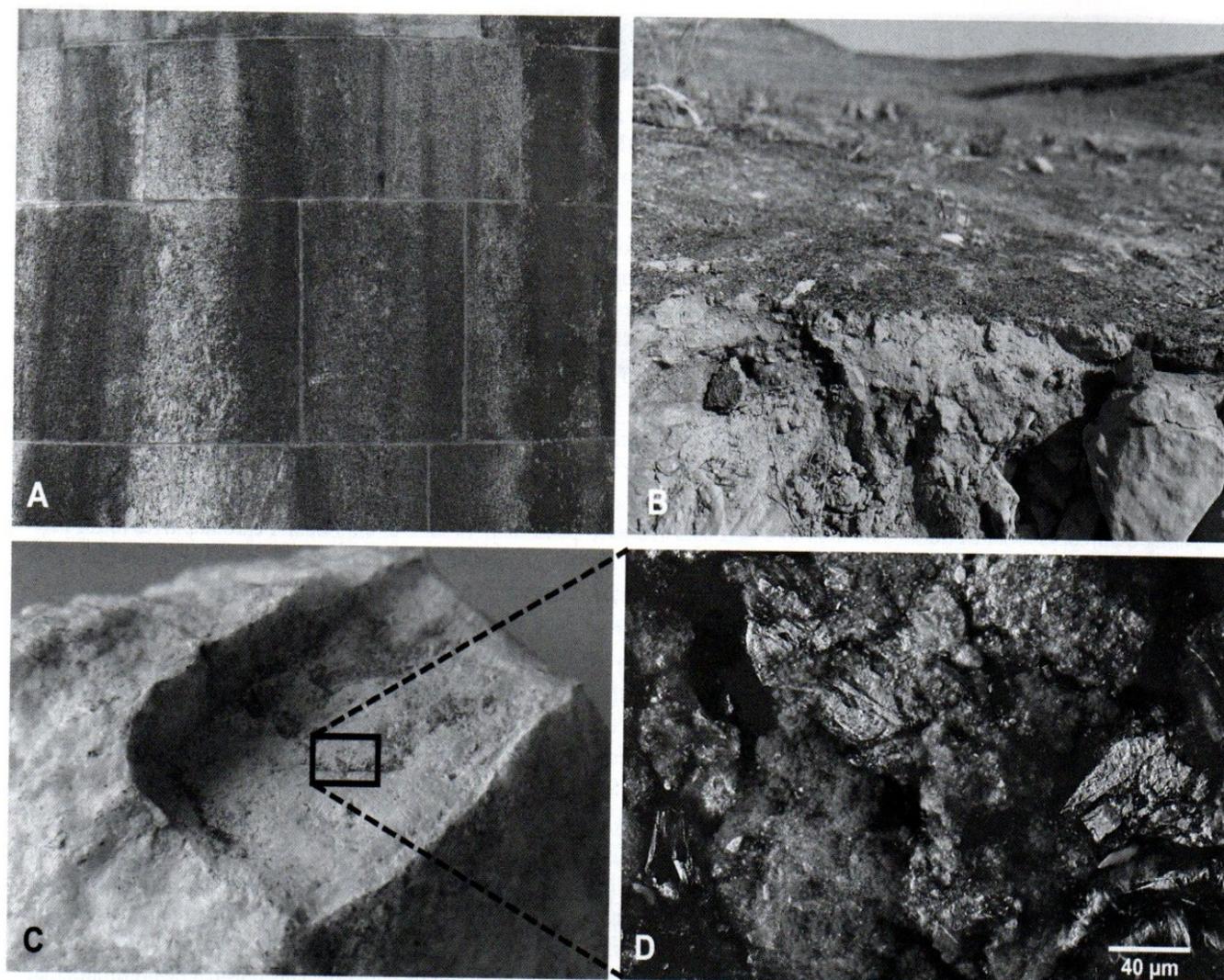


Figure 1. Colored SABs on mineral substrates. (a) green and purple SABs growing on a vertical wall of a stone monument in Milan, Italy. (b) a dark biocrust in the desert of the Dhofar Mountain of the Sultanate of Oman. (c) endolithic growth (green SAB) in a block of white marble used for construction. (d) Confocal laser scanning imaging of the endolithic biofilm. Red are microcolonies of photoautotrophic microbes, green are chemoheterotrophic microbes.

traits to community fitness and ecological dynamics. In other words, we would apply the concept of pigment ecology at the mineral–air interface to describe the SAB's requirement, environmental interaction, and effects on the ecosystems. To support our thesis, we review pigment-based colors of SAB-dwelling cells and their ecological significance by integrating research in microbiology, biogeochemistry, biogeomorphology, and microbial ecology. Evidence is drawn from various mineral–air ecosystems where microorganisms play crucial roles in primary productivity and global element cycles, such as biological soil crust (biocrust), topsoil, subaerially exposed rocks, and stone monuments.

This work provides the readers with an overview of the most relevant microbial pigments at the air–mineral interface, including photoreceptors in SAB color vision (box 1); an explanation of some of the evolutionary landscapes that make pigments adaptive strategies for resource allocation and survivability; a discussion of the multifaceted features of pigments that reflect the physiology and activities of SAB communities in different ecosystems, with a focus on the

pigmentation of stone heritage (box 2) and on paleobiology and astrobiology (box 3); a presentation of pigment ecology in microbial life-history strategies and coexistence theory; and a summary of key questions for future pigment-based ecology research and promising applications.

Microbial pigments and their role in the mineral–air interface

Pigments are chemical compounds that absorb light at certain wavelengths and reflect the others (Ramesh et al. 2019). All pigments contain conjugated moieties that allow electronic resonances and mediate energy transfer reactions in the cells. The pigments also serve multiple biological functions, such as energy harvest, photoprotection, free radical quenching, thermal stress protection, metal chelation, cell strength, desiccation, resistance, and cell development (Cordero and Casadevall 2017, Orlandi et al. 2021). Furthermore, the pigments are also involved in processes that underlie photomorphogenesis, photoperiodism, photomovement, and color vision through photoreceptor

Box 1. Color vision in microorganisms.

Just because we see through our eyes, it does not mean that eyeless microorganisms cannot perceive color. Perceived color depends on how an object absorbs and reflects light of a certain wavelength. The reflected light arrives in the retina, where it is transformed into electrical signals to be interpreted by the brain. So, we do not really “see” color but, rather, signals transmitted to our brain, which are converted by photoreceptors in our retinas.

Similarly, microorganisms can use their photoreceptors to transform the reflected light from a surface into a signal that indirectly informs the microorganisms about the substrate color. Photoreceptors are proteins covalently bonded to light-absorbing pigments called chromophores. On receiving the light signal, chromophores either change their conformation or undergo photoreduction to trigger biochemical signals for the transduction cascade (Fraikin et al. 2015, Multamäki et al. 2021). Putative light-sensing proteins are ubiquitously encoded in the genomes of chemotrophic, nonphotosynthetic bacteria and fungi (Herrera-Estrella and Horwitz 2007, van der Horst et al. 2007, Corrochano 2019).

Members of the phylum Cyanobacteria encode a vast array of photosensors, such as cyanobacteriochromes. Remarkably, the cyanobacteriochromes can be activated by different wavelengths that cover almost the entire light spectrum, from UV to near infrared (Bhaya 2016). For instance, *Nostoc* spp., a typical cyanobacterium of the mineral–air interface, has a red or far-red photosensor containing a phycocyanobilin chromophore that leverages light-triggered photoisomerization of bilin-bound chromophores to regulate gene expression, movement, and cell-to-cell communication (Xu et al. 2019, Moreno et al. 2020). The cyanobacteriochromes Cph1 and Cph2 contributed to the growth of *Synechocystis* in response to distinct wavelengths and intensities of light. Cph1 supports growth in far-red light and Cph2 modulates growth under red light (Fiedler et al. 2004).

Non-photosynthetic microorganisms such as fungi can sense near-ultraviolet, blue, green, red, and far-red light using up to 11 photoreceptors and signaling cascades to control gene expression and thereby improve fungal adaptation to environmental conditions (Yu and Fischer 2019). The genomes of black fungi belonging to the Eurotiomycetes, Dothideomycetes, and Lecanoromycetes, including lichen-forming species and rock-inhabiting extremotolerant species, contain multiple photoreceptors, suggesting that photoregulation is an important trait of fungal fitness at the mineral–air interface (Schumacher and Gorbushina 2020).

Although microbial photoreceptors are well known, only a few studies focused their attention on photoreceptors and color vision in microorganisms, especially at the mineral–air interface. The first attempt to illustrate the response of a microorganism to colors was carried out by Fernandez-Rodriguez and colleagues (2017). They designed a genetic circuit that enables *Escherichia coli* to use various wavelengths of light to control the multiple gene expression and produce red, green, and blue pigments. Once the bacterium was exposed to the colors red, green, and blue, the genetic circuit activated the production of the corresponding pigments. Therefore, by exposing the engineered *E. coli* strain to colored images, bacterial “photographs” could be obtained. This research demonstrates that bacteria can recognize a variety of colors by producing pigments that are the same color as the (reflected) light they are exposed to. Engineering bacteria with color vision could be useful in fine-tuning the control of biofilms in different medical and industrial settings.

Gambino and colleagues (2019) found that surface color affects SAB formation, where white and red substrates produced more biomass than blue and black. Differences in SAB growth were correlated to the differences in both quality (spectral composition) and quantity (photon flux) of the reflected light. Indeed, the biofilm growth on the white-bottom plates was supported by the highest intensity and the full spectrum of light. Meanwhile, the biofilms on the blue- and black-bottom plates experienced the lowest intensity and the filtered spectrum of light, which changed the red or far-red ratio received by the cells.

The influence of color on the primary bioreceptivity of granite to the terrestrial green alga *Apatococcus lobatus* was recently assessed (Sanmartín et al. 2020a). The results showed that granite with red hues favored the formation of subaerial microalgal communities compared with grey-hued granite. The red light reflected by the reddish surface is a well-known stimulus for photoreceptors in algae. The red or far-red light ratio increases photosynthetic yield stimulating chlorophyll production and cell growth in *Chlorella vulgaris* (Kula et al. 2014).

Altogether, these findings suggest that photosensors provide microorganisms with colored vision, consequently lending enormous capacity to fine-tune cellular responses to colored surfaces. Therefore, even microorganisms can “see” colors.

pigments (box 1). Therefore, microorganisms exploit light signals as a source of information regarding their location and surroundings, as well as a cue for acclimation and behavior.

The main pigments retrieved at the mineral–air interface are energy-related pigments such as chlorophylls (Chls), bacteriochlorophylls (BChls), rhodopsin, and phycobiliproteins, and protection-related pigments such as carotenoids, scytonemin, and melanins. Chemical structures and maximum absorbance wavelengths of the principal SABs’ pigments are reported in table 1. Pigment biosynthesis responds

to multiple environmental and physiological cues, such as temperature, oxygen supply, pH, light, ionic strength, and carbon and nitrogen sources.

Energy-related pigments. The variety of energy-related pigments reflects the need for microorganisms to evolve special photosystems to exploit any available spectral region with sufficient energy. Among the best-known energy-related pigments are the Chls from oxygenic phototrophs and the BChls and rhodopsin from the anoxygenic phototrophic prokaryotes (Chew and Bryant 2007). In addition, cyanobacteria and

Box 2. Relevance of SABs' pigmentation traits in stone heritage conservation.

Colorful microorganisms in form of SABs colonize the surfaces of outdoor stone monuments, mural paintings, archaeological surface findings, and rock art. Gaylarde and Gaylarde (2005) analyzed 230 SABs on a wide variety of building substrates around the world. They showed that phototrophs were the most abundant biomass in both Latin America and Europe, followed by pigmented fungi. Therefore, pigmentation is one of the most important phenotypic traits of SABs on monuments that reflect environmental adaptation to lithic surfaces in extreme conditions.

Thanks to the cyanobacteria predominance in many SABs on monuments, scytonemin is a widespread sunscreen pigment that allows microorganisms to self-protect from harmful UV and to survive desiccation before wetting and reanimation (Keshari and Adhikary 2013). Cappitelli and colleagues (2012) reported that some areas of the National Museum of the American Indian building (Washington, DC, in the United States) contained a high content of scytonemin, likely by the cyanobacteria *Gloeocapsa* and *Lyngbya*. Similarly, scytonemin was more abundant than carotene and Chla in all SABs sampled from eight historical monuments of Varanasi (India; Pathak et al. 2017). Recently, Mondal and colleagues (2022) found the reduced form of scytonemin in the cyanobacteria *Brasilonema* sp. from the monuments of Santiniketan and Bishnupur (India).

Pigmentation can be affected by materials, locations, environmental conditions, structure, and dynamics of microbial communities. Gaylarde and Baptista-Neto (2021) stated that dark brown or black stains and orange-yellow patinas can be produced by both bacteria and fungi, whereas the surface humidity strongly affects the SAB components and colors. For instance, the red color produced by the overgrowth of carotenoid-producing alga *Trentepohlia* was seen on north- and east-facing walls of the Rio Bec style Mayan buildings in Campeche state, Mexico. Grey or black biofilms, a color characteristic of UV-resistant cyanobacteria (mainly *Gloeocapsa* and *Chroococciopsis*), colonized the sun-exposed areas of the buildings. There was no evidence that stone degradation was occurring beneath the colored biofilms (Ortega-Morales et al. 2013). Two areas of a fort in Niteroi, Rio de Janeiro, showed different colored SABs according to the climatic and positional factors: a dark green-brown biofilm below leaking pipes containing filamentous anoxygenic phototrophs, whereas a grey-pale-green dry biofilm was mainly non-photosynthetic Proteobacteria (Ogawa et al. 2017).

Within biodeterioration processes, a rosy alteration is a widespread phenomenon on both lithic and painted surfaces. The phenomenon was related mainly to the presence of cyanobacteria (Cappitelli et al. 2009) and algae (Ortega-Morales et al. 2013, Bartoli et al. 2019) and extremophiles (alkaliphilic, thermophilic, and halophilic microorganisms) that produce carotenoids (Imperi et al. 2007, De Felice et al. 2010, Ettenauer et al. 2014, Gomoiu et al. 2017, Cojoc et al. 2019, Leplat et al. 2019). The common link among different monuments colonized by pink biofilms (due to carotenoids) seems to be the crystallization of salts aided by water infiltration, which creates an optimal condition for the growth of the halophilic microorganisms (Ettenauer et al. 2014). Carotenoids are known to act as membrane stabilizers against salt stress (Seel et al. 2020).

Although pigments are instrumental in supporting microbial life, the discoloration of stone surfaces is often disconcerting. However, not all colored biofilms are detrimental to the mineral substrates (Pinna 2014, Gulotta et al. 2018) and their removal may cause irreversible damage. As an iconic example, the processional cloister of the Monastery of San Martiño Pinario (Santiago de Compostela, Spain) was colonized by a green highly hydrophobic SAB that acted as a natural waterproofing agent for the building (Sanmartín et al. 2020b). This biofilm was mainly formed by *Apatococcus lobatus* (Chodat) J.B.Petersen (Chlorophyta), and it was proven to only have an aesthetic impact, without damaging or protecting the substrate. The researchers recommended not removing the existing green SABs according to the minimal intervention concept.

The 46,000-year-old Bradshaw rock art, often exposed to sun and rain, can be vivid with high contrast, even though it has never been repainted. Pettigrew and colleagues (2010) reported that the original paint is no longer present in this rock art but has been replaced by a living pigmented SAB, which naturally contributes to the longevity and vividness of these ancient paintings. The nutrients contained in the original paint kickstarted a mutual relationship between black fungi and red cyanobacteria. The fungi can provide water to the bacteria, whereas the bacteria provide carbohydrates to the fungi. The black fungi were identified as *Chaetothyriales*, an extremely conservative rock-adapted taxon that replicate by cannibalizing their predecessors *in situ* but remained strictly within the art's boundaries.

Therefore, although the presence of SABs on mineral surfaces implies current or past interactions with the substrates, its presence is not necessarily biodegradative as is frequently thought (Favero-Longo and Viles 2020). Because the correlation between SABs and stone decay is a matter of controversy, the proper understanding of the SABs' role is instrumental to the sustainability of stone heritage management. Biopigments offer an indication of a specific condition of the SAB community. For this reason, we hypothesize that SAB's color can be exploited to categorize the SAB's impact on monuments on the basis of their deteriorative, neutral, or protective roles. To this end, a mathematical correlation between SABs' color fingerprints and multidisciplinary investigations on monuments—used to characterize the deteriorative, neutral, and bioprotective roles of SABs under different conditions—should be carried out. Once this correlation is established, heritage professionals could simply read *in situ* the SAB's color and use it as a bioindicator of SABs' impacts on the stone.

By exploiting the SAB color as a benchmark of stone biodecay, a simple and nondestructive monitoring tool with an easy to understand language, the color will be provided to those who preserve the cultural heritage.

red algae also synthesize accessory light-harvesting pigment molecules called phycobiliproteins (Adir et al. 2020, Puzorjov and McCormick 2020). There are four types of phycobiliproteins based on their maxima light absorption peak: phycoerythrin (red pigment), phycocyanin (blue pigment), phycoerythrocyanin (orange pigment), and allophycocyanin (bluish green pigment; Pagels et al. 2019). Phycocyanin and allophycocyanin are present in all cyanobacteria worldwide, whereas phycoerythrin and phycoerythrocyanin have a limited distribution in cyanobacteria (Bryant 1982). Depending on cyanobacteria habitats the ratio of these pigments can vary (Murton et al. 2017). Phycobiliproteins have been shown to display antioxidative and radical-scavenging activity. It has been observed that the intracellular content of each specific phycobiliprotein depends on the incident light intensity, suggesting different roles of phycobiliproteins in light dissipation in a photon-excessive condition (Montero-Lobato et al. 2020). The resources dedicated to phycobiliproteins synthesis are as much as 60% of the total soluble cellular protein, proving the substantial fitness benefits of producing these pigments (Wiltbank and Kehoe 2019).

Although Chls in cyanobacteria and other oxygenic photoautotrophs absorb light primarily at 514–700 nanometers (nm), BChla in aerobic anoxygenic phototrophic bacteria can absorb near-infrared light at 760–1130 nm with minimum absorption of the visible red (Tang et al. 2018). BChla-containing bacteria have been found in rock varnish communities (Kuhlman et al. 2006), biocrust (Csotonyi et al. 2010), oligotrophic soils from the Sør Rondane Mountains (2016a, Tahon et al. 2016b, Tahon and Willems 2017) and the Himalaya plateau (Rehakova et al. 2019). These microorganisms can use both organic and inorganic electron donors for light-dependent fixation of carbon dioxide without generating oxygen (George et al. 2020).

Chls pigments display a very low degree of light absorption in the range of 500–600 nm, an energy-rich region of the solar spectrum (Kume et al. 2018). By contrast, microbial rhodopsins show a strong well-defined peak of absorbance centered at a 568 nm (DasSarma and Schwieterman 2021). Microbial rhodopsins are a family of transmembrane proteins that contain opsin and a covalently bound retinal cofactor as a chromophore. Microbial rhodopsins have two main biological functions: as light-driven proton pumps, which respond to light by transporting ions across the cell membrane and generating a chemiosmotic potential for ATP (adenosine triphosphate) synthesis, and as photo-sensory receptors that mediate light-induced behavioral responses (Govorunova et al. 2017). The dissemination and diversification of microbial rhodopsins across Archaea and Bacteria can be explained by considering the minimal genetic determinants of rhodopsins synthesis (a single opsin gene and another gene for retinal synthesis from carotenoid) subjected to horizontal gene transfer. A recent metagenomic study of soil crusts showed that half of the microbial genomes encode for rhodopsins (Finkel et al. 2013), whereas 20% of bacterial taxa of hypolithic communities

(the assemblages found below translucent rocks) in the Antarctic Dry Valley harbored rhodopsin genes (Guerrero et al. 2017). The presence of actino-opsin genes in the genome of Actinobacteria—one of the most abundant phyla in the SABs—indicates the microorganisms' ability to boost heterotrophic growth via phototrophy (Chuon et al. 2021). This new insight reveals the microorganisms' coping mechanism in the harsh and energy-deficient mineral–air interface, which is by maximally exploiting solar energy. BChl- and rhodopsins-based phototrophy ensure heterotrophs meet the energy demand during starvation conditions by using sunlight as an alternative energy source, which is an important energetic mechanism underpinning the microbial function in desert ecosystems (Leung et al. 2020). In addition, the widespread distribution of prokaryotic rhodopsins on Earth and their capacity to generate chemical energy using an energy-rich portion of the electromagnetic spectrum suggest the early appearance of these biopigments on our planet (DasSarma and Schwieterman 2021). Recently, BChl- and rhodopsin-based dual phototrophy has been observed in Alphaproteobacteria isolated from the “Lille Firn” glacier and the nearby exposed soil in northeast Greenland (Zeng et al. 2020). This process would reduce the consumption of organic matter for energy production in bacteria by increasing flexibility and efficiency in conserving light energy. Such diversity of photosynthetic pigments is instrumental for efficiently capturing the available light spectrum and, therefore, for determining the distribution and composition of SAB communities. The pigment set increases the survival and fitness of phototrophs by allowing microorganisms to capture light that is unused by others in their local environment. This is a widely used practice in a natural environment where microorganisms must compete with their neighbors for space and resources.

Protection-related pigments. Carotenoids are organic liposoluble pigments produced by bacteria, archaea, algae, and fungi, whose colors range from yellow to purple. Carotenoids include over 1100 substances belonging to isoprenoids, which are characterized by the presence of a conjugated tetraterpene (C40). Carotenoid production in some non-phototrophic bacteria occurs in a light-dependent manner to protect cells from photooxidants (Sumi et al. 2019). The conjugated double bonds are responsible for the photoprotective and antioxidative mechanisms of the carotenoids. Carotenoids scavenge oxygen radicals by releasing energy through polyene chain vibration (physical reaction), but recent research revealed their ability to inhibit these radicals through chemical reactions (Maoka 2020). For instance, astaxanthin can react with peroxyxynitrite and nitrogen dioxide radicals to form nitroastaxanthin to prevent the nitration of tyrosine. Similar results were obtained in cases of beta-carotene, lutein, zeaxanthin, capsanthin, and fucoxanthin (Maoka 2020).

Other protective pigments include potent sunscreens—namely, scytonemin and melanins. The alkaloid biomolecule

Box 3. Biopigments in paleobiology and astrobiology.

Paleobiology—the investigations about the origin and evolution of life on our planet—has strong connections with astrobiology—the studies on the existence of life in other parts of the cosmos. Both disciplines seek to detect putative extinct or even extant life forms on the Earth and exoplanets by studying biosignatures—universal molecules considered as the fingerprints of the past or the present biological activity.

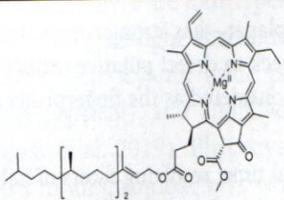
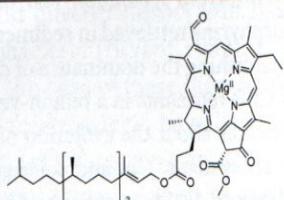
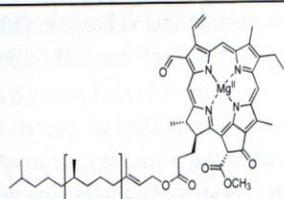
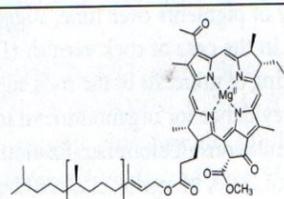
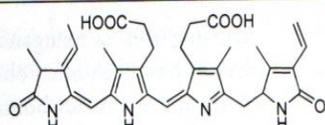
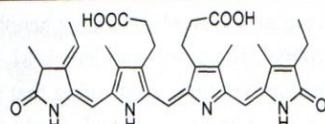
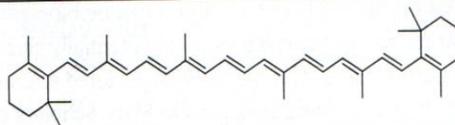
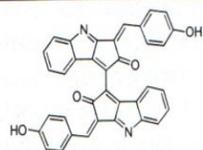
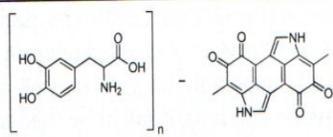
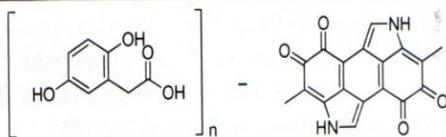
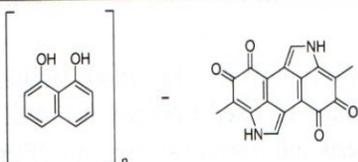
Microbial pigments can persist and be recognized over vast spans of geological time, resolving facets of paleobiology and evolution. Gueneli and colleagues (2018) discovered molecular fossils of Chls, the porphyrins, from 1.1-billion-year-old marine black shales of the Taoudeni Basin (Mauritania). By measuring the nitrogen isotope ratios of porphyrins retrieved in sedimentary rocks, the researchers were able to quantify the abundance of different phototrophs in the ocean, establishing the dominance of cyanobacteria over planktonic algae. Sforza and colleagues (2022) discovered *in situ* the first evidence of Chls remnants in a billion-year-old multicellular algal microfossil preserved in shales from the Congo Basin. The result provides new clues about the evolution of eukaryotic phototrophy during the Precambrian and the diversification of primary producers in early ecosystems. Cui and colleagues (2020) reported that carotenoids from green sulfur bacteria dominated in Phanerozoic marine sediments, whereas cyanobacterial aromatic carotenoids dominated in phanerozoic lacustrine settings with low sulfate inventories. Vinnichenko and colleagues (2020) reported the discovery of degradation and isomerization products of carotenoids from carbonaceous shales of the 1.73-billion-year-old Wologorang Formation in the southern McArthur Basin. Therefore, the findings extend the biomarker record of phototrophic bacteria by approximately 90 million years. Altogether, these results show how fossil microbial pigments, exemplified by carotenoids and Chls, capture the history of Earth's aquatic primary producers. The succession of primary producers in the oceans is instrumental to understanding the marine ecology throughout the Earth's history. Moreover, the role of pigments is crucial in the interaction between the host rock and the community (Krumbein et al. 2003). Many studies also explore the stability of pigments over time, suggesting that pigmentation of rock surfaces can survive after the disappearance of the SAB community as in the case of rock varnish (Dorn 1998). Within rock varnishes and crusts, organomineral interactions occur, resulting in the weathering of minerals of the rock support and neoformations of secondary minerals (Dorn and Oberlander 1981a, 1981b, Dorn 2007). Such evidence for organomineral interactions can be found in fossil rock varnish millennia after the decay of the SAB community as accumulations of biomineralization products or amorphous organics, or as casts of pristine biological features as hyphae (Dorn 2007, Zerboni 2008, Mergelov et al. 2012); in both cases, the result is the stabilization of the color of the rock surface over time.

Many of the rocks on Mars' surface display reddish to dark shiny surface coatings resembling iron- or manganese-rich terrestrial rock varnish. In desert rock varnish, a combination of dark pigments with metal oxihydroxides has been often observed (Dorn 1998). It has been demonstrated that most of the color of rock coatings is produced by microbial pigments firmly bound to the rock particles (Gorbushina 2007). Therefore, pigments produced by varnish microorganisms may play important roles in coating morphogenesis and distribution (Kuhlman et al. 2006). This is not surprising, because some pigments, especially dark phenol-containing pigments, are associated with the accumulation of metals (Hong and Simon 2007). Krumbein (Krumbein and Jens 1981, Krumbein et al. 2003) studied the accumulation of dark pigments and iron or manganese oxihydroxides over time, confirming that it takes 10^3 years for a thick desert varnish to form. Based on these considerations, if desert varnish on Earth has mostly a biological origin, the identification of corresponding biomarkers for extraterrestrial life could foster studies on Mars. These biomarkers can be biopigments. Preserved biopigments not only yield interpretations on the appearance of ancient microorganisms but can also potentially elucidate their ecology and behavior, giving clues to potential targets in the search for extraterrestrial life (Lindgren 2016). Colored microorganisms have been identified in many extreme environments of our planet, which are often considered analogous to Mars. Scholars are investigating extreme ecological niches on Earth (in hot and cold deserts, namely the Dry valleys of Antarctica and the Atacama) as analogous to Mars's surface. For instance, desert-inhabiting microcolonial fungi—which were discovered in the early 1980s (Krumbein and Jens 1981, Friedmann 1982, Staley et al. 1982)—are examples of eukaryotes with the bewildering capacity to adapt to extraterrestrial conditions. Microcolonial fungi synthesize a mix of UV-absorbing and antioxidant pigments (carotenoids, melanin, and mycosporines) that convey multiple stress resistance to desiccation, temperature, and irradiation changes. Recent work reported the persistence of fungal melanin in Martian rock analogs after exposure to space and Mars-like conditions (Pacelli et al. 2020). This finding suggested that the production of UV-protecting pigments can be part of microbial survival strategies on Mars. Bacteriorhodopsin may potentially serve as remote biosignatures for life outside the solar system. Because the bacteriorhodopsin shows a strong well-defined peak of absorbance at 568 nm, which is complementary to that of Chl pigments (approximately 700 nm), it might be used to compare the remote signatures of rhodopsin-like phototrophy with those produced by Chl-based photosynthesis analogs on exoplanets (DasSarma and Schwieterman 2021). Therefore, these retinal-based proteins are potential biosignatures for extraterrestrial life, whose unique spectral profiles can be caught by next-generation space-based telescopes. Nonphotosynthetic pigments in the extremophiles can also be used as potential surface biosignatures for exoplanets research (Schwieterman et al. 2015). Recently, Sharma (2020) used computational models to invent novel pigments and simulate their spectral profiles for the identification of extraterrestrial life.

scytonemin is a yellow-to-brown extracellular pigment produced only by certain strains of sheathed or encapsulated cyanobacteria (Garcia-Pichel and Castenholz 1991, Rastogi et al. 2015). Certain environmental stresses such

as UVA (ultraviolet) radiation, temperature, periodic desiccation, and fixed-nitrogen deficiency can modulate the synthesis and levels of scytonemin (Fleming and Castenholz 2007, Sorrels et al. 2009, Orellana et al. 2020). In Atacama

Table 1. Chemical structures, maximum absorbance wavelengths, functions, and microorganisms of the SAB-relevant pigments.

Chemical structure	Details
	<p>Chlorophyll a</p> <ul style="list-style-type: none"> • Absorption peak: 642 nm and 372 nm. • Role: energy harvest. • Microorganisms: cyanobacteria and algae.
	<p>Chlorophyll b</p> <ul style="list-style-type: none"> • Absorption peak: 626 nm and 392 nm. • Role: energy harvest. • Microorganisms: cyanobacteria and algae.
	<p>Chlorophyll f</p> <ul style="list-style-type: none"> • Absorption peak: 706 nm. • Role: energy harvest. • Microorganisms: cyanobacteria, red algae and other oxygenic microorganisms.
	<p>Bacteriochlorophyll a</p> <ul style="list-style-type: none"> • Absorption peak: 805 nm and 870 nm. • Role: energy harvest. • Microorganisms: purple and green sulfur bacteria and some groups of aerobic bacteria, such as members of the <i>Acidiphilium</i> genus.
	<p>Phycoerythrobilin</p> <ul style="list-style-type: none"> • Absorption peak: 530–570 nm. • Role: energy harvest, antioxidative and radical-scavenging activity. • Microorganisms: cyanobacteria and algae.
	<p>Phycocyanobilin</p> <ul style="list-style-type: none"> • Absorption peak: 640–660 nm. • Role: energy harvest, antioxidative and radical-scavenging activity. • Microorganisms: cyanobacteria and algae
	<p>β-carotene</p> <ul style="list-style-type: none"> • Absorption peak: 448 nm. • Role: energy harvest, antioxidative and radical-scavenging activity. • Microorganisms: bacteria, algae and fungi.
	<p>Scytonemin</p> <ul style="list-style-type: none"> • Absorption peak: 252 nm, 278 nm, 300 nm, 384 nm. • Role: photoprotection, free radical quenching, thermal stress protection, desiccation. • Microorganisms: cyanobacteria and algal symbionts of some lichens.
	<p>DOPA-melanin</p> <ul style="list-style-type: none"> • Absorption peak: 300–600 nm. • Role: photoprotection, free radical quenching, thermal stress protection, metal chelation, cell strength, desiccation, resistance. • Microorganisms: bacteria and fungi.
	<p>Pyromelanin</p> <ul style="list-style-type: none"> • Absorption peak: 200–300 nm • Role: photoprotection, free radical quenching, thermal stress protection, metal chelation, cell strength, desiccation, resistance. • Microorganisms: bacteria and fungi.
	<p>DHN-melanin</p> <ul style="list-style-type: none"> • Absorption peak: 300–600 nm. • Role: photoprotection, free radical quenching, thermal stress protection, metal chelation, cell strength, desiccation, resistance, and cell development. • Microorganisms: bacteria and fungi.

halites under natural solar radiation, epilithic (rock surface) cyanobacteria had a scytonemin content 12 times higher than their endolithic (rock pores) counterparts (Vitek et al. 2014). Gao and colleagues (2021) reported that this pigment can prevent up to 90% of the incident solar UV radiation from entering the cell, by absorbing short wavelength UV radiation and dissipating energy through harmless thermal deexcitation. However, the localized warming caused by the accumulation of scytonemin, and the thermal deexcitation are not without consequences. Couradeau and colleagues (2016) showed that scytonemin in mature biocrusts can increase the soil surface temperature by as much as 10 degrees Celsius, which replaces thermosensitive bacterial species with thermotolerant microorganisms. Therefore, scytonemin shapes the composition of the SAB communities indirectly. Scytonemin also serves as a potent antioxidant that prevents cellular damage caused by reactive oxygen species (Matsui et al. 2012).

Melanin is a general term for a group of heterogeneous polyphenols produced by a variety of organisms including bacteria and fungi (Tran-Ly et al. 2020). Microbial melanin is classified into two types: allomelanin and eumelanin. Allomelanin encompasses a variety of non-nitrogenous subgroups of melanin derived from different catecholic and dihydroxynaphthalene precursors, which are known as 1,8-dihydroxynaphthalene melanin and pyomelanin. Eumelanin includes 3,4-dihydroxyphenylalanine melanin, which is synthesized via a similar pathway as mammalian melanin synthesis (Singh et al. 2021). These dark pigments are characterized by their unique physicochemical properties such as broadband optical absorption, paramagnetism, charge transport, and remarkable structural stability, which confer diverse biological functions. Microbial melanization is used for photoprotection, thermoregulation, energy harvest, free radical quenching, metal chelation, cell strength, and resistance to desiccation (Pavan et al. 2020). For instance, the presence of a thicker melanized cell wall increases the resistance of fungi to acute and chronic ionizing radiation (Pacelli et al. 2020, Liu et al. 2021) and bolsters fungal cell-wall strength, which enhances the fungi's penetration into mineral substrates (Liu et al. 2020b, Prenafeta-Boldú et al. 2022). Similar to scytonemin, the role of melanin in thermoregulation stems from its ability to effectively absorb solar radiation and dissipate it non-radiatively in the form of heat. Cordero and colleagues (2018) studied the distribution of 358 isolated fungal species worldwide and found the first empirical evidence of a geographical pattern in color lightness. They reported that color lightness, because it decreased from the equator to the poles, is relevant for the thermoregulation of fungi. Recently, untargeted metabolomics revealed an increase in melanin expression in southern communities on exposed rocks, which confers high tolerance for low temperature and drought (Coleine et al. 2020). These findings suggest the significance of thermal melanism for the evolution of eukaryotic life, because it represents another important mechanism that enabled the

earliest terrestrial organisms to survive and grow alongside photosynthesis. Besides thermoregulation, melanin is also involved in energy transduction in a process called radiosynthesis, where it harvests energy from electromagnetic radiation for metabolic use using the electrical properties (Casadevall et al. 2017).

Although the sunscreen pigments chemically and physically protect the producing microorganisms, the protection is extended to other cells in proximity. Mature biocrusts display pigments stratification with the highest concentrations of mycosporin-like amino acids, scytonemin, and carotenoids in the upper layers, whereas Chl_a and phycobiliproteins are in the lower portions. In line with the pigments' stratification, biocrusts from the Needles District of the Canyonlands National Park presented dark-pigmented *Nostoc* spp. and *Scytonema myochrous* restricted to the soil surface and motile filamentous *Microcoleus vaginatus* extending underneath (Bowker et al. 2002). *M. vaginatus* showed significant mortality without *Nostoc* spp. and *S. myochrous*, suggesting that the sunscreen pigments produced by *Nostoc* and *Scytonema* in the crust surface protected the less-pigmented *M. vaginatus* from the photobleaching (Bowker et al. 2002). In Antarctic endolithic ecosystems, melanized fungi form a black sunscreen above the photobiont stratification to protect the whole community (Selbmann et al. 2013). Similarly, the relative enrichment of scytonemin in the black layer on the halite crust surface was documented by Vitek and colleagues (2014). Scytonemin is a very stable pigment that remains intact within the extracellular polymeric matrix (EPM), conferring passive UV protection to both metabolically active and inactive cells. Moreover, the scytonemin-rich layer acts as a screen for the Chl-rich layer located below. Interestingly, Vitek and colleagues (2014) noted that the Chl-rich layer underneath was composed of the same cyanobacterial taxa as the black layer but lacking in scytonemin. They concluded that, because the biosynthesis of scytonemin is an energy-consuming process, the protective black layer allowed the underlying cells to minimize energy expenditure for scytonemin biosynthesis.

Analytical techniques for studying pigments. A fine characterization of the microbial pigments is the first step in disentangling the complex phenomena behind the multiple biological functions of an SAB's color. Various analytical techniques developed over the years are still in use to detect and analyze microbial pigments. Pigments extraction from SABs followed by separation with chromatography (e.g., high-performance liquid chromatographic) and identification or quantification with mass spectrometry, and nuclear magnetic resonance are techniques largely used for studying pigments, even at trace levels (Cappitelli et al. 2012, Keshari and Adhikary 2013, Montero-Lobato et al. 2020). Flow cytometry has been occasionally applied to microbial colonization on heritage samples to study fluorescence produced by photosynthetic pigments (Cappitelli et al. 2009). In recent years, Raman spectroscopy has become a popular

analytical tool for the qualitative and quantitative assessment of microbial pigments in the SABs (Vitek et al. 2017, 2020). The researchers in such studies have used high-resolution laboratory Raman spectrometers and more recently, portable handheld instruments that can be used in the field. Raman microspectrometry has allowed the direct study of pigment type and distribution in endolithic zones without sample treatment or extractions. The investigations revealed differences in pigment distribution in SABs colonizing differing lithotypes such as dolomite, gypsum, or altered orthoquartzite (Edwards et al. 2005, 2007). Raman microspectrometry was able to detect SAB pigments such as melanin, scytonemin, chlorophyll, and carotenoids in samples of halite endoliths from the Atacama Desert, in Chile (Vitek et al. 2010, Culka et al. 2017). Importantly, Raman spectroscopy reliably identifies pigments but cannot identify the producing species, because the same pigment may be produced by more than one species. It is the combination of molecular investigations and Raman spectroscopy that provides such an association (Imperi et al. 2007).

SAB's pigmentation as an adaptive strategy for resource allocation and survivability

The color change manifested by pigment production is a form of phenotypic plasticity, which confers fitness advantages to the whole microbial community by optimizing resource allocation. From an adaptation standpoint, pigments can serve several functions, and the resulting change in color patterns frequently represent a trade-off between the different evolutionary drivers, such as light quantity (irradiance) and quality (wavelength). These trade-offs can vary even within the population, and the color can be altered strategically according to the condition and the purpose. At the mineral–air interface, differences in light quality are not only related to the daylight or annual cycles but also to the system condition that constrains part of the spectrum (e.g., transmittance and lithology) to be available to the microorganisms. A Monte Carlo model of light propagation in translucent rocks described the light levels at the bottom and the subsurface edges of desert quartz. The model showed the variation in light levels, with the available light resulting higher at the sunward subsurface edge than at the basal surface (Jolitz and McKay 2013). Meslier and colleagues (2018) observed that different lithologies (limestone, gypsum, ignimbrite, and granite) collected in the Atacama Desert have different light transmission properties. The solar irradiance transmission spectra measured at the ventral surfaces of quartz stones in the Namib Desert showed complete comminution of the short wavelengths (UV and blue) and higher transmission in the longer wavelength (Gwizdala et al. 2021). Therefore, the hypolithic communities of mineral substrates experience reduced illumination and a relatively red-enriched light. Overall, this light-filtering process yields a series of distinct spectral niches for phototrophic microorganisms, leading to the development of different spectrum-response mechanisms. To this end, pigments contribute to the acclimation

(short term) and adaptation (long term) of microorganisms to light variability.

Fast spectrum-response strategies include the mechanisms for dissipating the excess excitation energy from the light-harvesting complexes in the form of heat. It is well known that cyanobacteria use sophisticated molecular machinery composed of light-harvesting complexes, energy-converting photosystems, electron carriers, and regulatory complexes, to convert photosynthetically active radiation into chemical energy in the thylakoid membranes (Stirbet et al. 2020). The complexity of this molecular machinery makes photosynthetic organisms sensitive to fluctuating light intensities. Indeed, light becomes dangerous when the entire photosynthetic electron transport chain becomes excessively reduced, forming reactive oxygen species that leads to severe cell damage. Therefore, the survival and growth of photosynthetic microorganisms strongly depend on the balance between the collection of light energy for photosynthesis and protection against photooxidation. As an example of a fast acclimation process, the orange carotenoid protein (OCP) of cyanobacteria senses light intensity and induces thermal dissipation of excess excitation energy by interacting with the phycobilisome (Muzzopappa and Kirilovsky 2020). By studying the pigments of an endolithic cyanobacterial community along an ignimbrite cross-section profile, Vitek and colleagues (2017) reported the Raman shifts of the $\nu_1(\text{C}=\text{C})$ carotenoid band positions with respect to the depth. The findings suggested that red-shifted carotenoids (OCP–OCP^R transition) in endolithic *Chroococcidiopsis* sp. in proximity to the surface is a light-dependent phenomenon. This was interpreted as *Chroococcidiopsis* sp.'s photoprotection to cope with the excess light near the rock surface.

One of the best-characterized spectrum-response strategies is chromatic acclimation, in which cyanobacteria modulate the composition of primary pigments in their photosynthetic light-harvesting antennae (phycobilisomes) to compensate for light quality changes (Sanfilippo et al. 2019). Therefore, chromatic acclimation involves tuning the cellular metabolism and physiology to external light cues through pigment alteration. During chromatic acclimation, the synthesis of phycoerythrin partially replaces phycocyanin in the phycobilisome complexes, leading cyanobacteria to use a significantly greater amount of green light for the photosynthesis (Hirose et al. 2019). Therefore, cyanobacteria can appear in different colors on the basis of the light they endure, with red and green light causing the cells to turn blue-green and brick red, respectively. The regulation of this photoreversible color change involves sophisticated light-color-sensing and signal-transduction systems (Kehoe and Gutu 2006). The chromatic acclimation process is generally slower than OCP because it involves gene expression changes and the synthesis of new protein complexes and pigments. Smith and colleagues (2014) suggested that chromatic acclimation takes place in cyanobacteria that colonize hypolithic substrates from the Mojave Desert. A red shift in the spectral emission profiles of *Chroococcidiopsis* cells

inhabiting quartz, carbonate, and talc was observed and correlated to the modification of the phycobilisome composition (Smith et al. 2014).

One of the most recently identified forms of chromatic acclimation is the far-red light photoacclimation (FaRLiP). During this acclimation, cyanobacteria remodel photosystems and phycobilisomes while synthesizing atypical Chls (Chl*d* or Chl*f*) and far-red-absorbing phycobiliproteins (Gan Fei et al. 2014). Although FaRLiP reduces photosystem efficiency, it allows cyanobacteria to sustain photosynthetic activity under conditions where photosynthetically active radiation is limited and energy yield from normal photosynthesis is compromised (i.e., Chl*a* based). FaRLiP is instrumental to terrestrial cyanobacteria because they frequently occur in niches where visible light is strongly filtered or scattered, leading to enrichment in wavelengths longer than 700 nm. A Chl*f*-containing cyanobacterium with the capability of near infrared-driven oxygenic photosynthesis was found on moist limestone outside Jenolan Caves in Australia (Behrendt et al. 2015). Recently, Antonaru and colleagues (2020) used the marker gene *apcE2*—which encodes a phycobilisome linker associated with far-red light photosynthesis—to detect Chl*f* microorganisms in metagenomic data from environmental samples. The results showed the presence of the gene in cyanobacteria commonly retrieved at the mineral–air interface and producing Chl*f*, such as *Chroococcidiopsis* sp. and *Calothrix* sp. Furthermore, the study highlighted the distribution of Chl*f*-containing cyanobacteria in a variety of habitats at the mineral–air interface across the globe, such as the Frasassi Cave, in Italy, and soils in Germany and Cuba (Antonaru et al. 2020).

Gwizdala and colleagues (2021) stated that neither complementary chromatic adaptation nor FaRLiP were adaptation mechanisms used by hypolithic cyanobacteria inhabiting quartz pebbles in the Namib Desert. The researchers did not detect any Chl*d* or Chl*f* in SAB pigment extracts, and they did not identify any open reading frames mapping to phycoerythrin, suggesting that other mechanisms could have been adopted by the hypolithic cyanobacteria to respond to light stress. Similar studies reported the lack of redshifted Chls in hypoliths while observing an increase in phycobiliproteins (Smith et al. 2014, Mehda et al. 2022). These findings were interpreted as the response of cyanobacteria to low-light conditions in the deeper part of the colonized rocks. Therefore, an alternative to FaRLiP is the low-light photoacclimation, where cyanobacteria remodel their photosynthetic apparatus to absorb light beyond the wavelength of 700 nm to increase their light-harvesting capacity.

The chromatic tuning ability of SAB-dwelling cells provides enormous flexibility in adjusting cellular response to light and redox conditions. Therefore, change in pigmentation can be used to maximize energy collection for photosynthesis or to protect the photosynthetic apparatus, guaranteeing the level of organic carbon for the sustainability of the whole community. Because organic carbon

availability is the highest during the day when photosynthesis is the most active, if a microorganism can use sunlight as a sensor to initiate carbohydrates transport and metabolism, it could theoretically gain a growth advantage over the other components of the SAB community. Maresca and colleagues (2019) reported that some actinobacteria use light as a signal for synchronizing their metabolism with their phototrophic neighbor, maximizing organic carbon uptake at the moment photosynthates are released. This fine control was enabled by cryptochromes—flavin pigments that control the circadian rhythm—that sense specific wavelengths of light. Because of actinobacteria's abundance in SAB, it seems that the regulation of sugar metabolism is a mechanism to efficiently use the nutrients excreted by phototrophs, which are plenty at the mineral–air interface.

Pigmentation as a reflection of SAB physiology and activity

Microbial pigments are not merely colors; they possess multifaceted features that reflect the physiology and activities of the SAB communities. Therefore, pigments can provide detailed information about the stochastic response of SABs to climatic and environmental conditions. Therefore, SAB's pigments may be applied as a tool for biodiversity conservation strategies, ecosystem functioning, ecological modeling, and climate change monitoring.

Discrete color phenotypes are often associated with differences in morphological, physiological, and behavioral traits. For instance, chlorosis is the acclimation process pursued by nondiazotrophic cyanobacteria in response to nitrogen shortage. During nitrogen starvation, the cells gradually turn down their metabolism and enter a dormant-like state characterized by minimum photosynthesis and pigmentation, which allows long-term survival with resuscitation under favorable environmental conditions (Spät et al. 2018). A hallmark of chlorosis is the rapid proteolytic degradation of phycobiliproteins—the major light-harvesting pigments in red algae and most cyanobacteria—accompanied by cell color change from blue-green to yellow. It has been shown that phycobiliproteins degradation favors the release of soluble amino acids and reduces the intracellular reactive oxygen species level by decreasing the light absorption capability (Forchhammer and Schwarz 2019, Krauspe et al. 2021). The current understanding of the chlorotic cells' regulatory processes depicts the intricate mechanism that modulates ribosomal proteins, RuBisCO (ribulose-1,5-bisphosphate carboxylase-oxygenase) components, central regulators, and metabolic enzymes, as well as hyperphosphorylation of nondegraded phycobiliproteins (Spät et al. 2018, Krauspe et al. 2021a). The degradation and resynthesis of phycobiliproteins were examined using hyperspectral confocal fluorescence microscopy coupled with single-cell analysis on the basis of the pigment content and localization in live cyanobacterial cells (Murton et al. 2017). The findings revealed that phycobiliproteins degradation and resynthesis are coordinated by highly synchronized cells that undergo

pigment modifications. Chl fluorescence was decreasing during nitrogen starvation without any change in the localization of subcellular Chl.

Chla detection and quantification have been used to characterize biocrust development (Caesar et al. 2018, Román et al. 2021) and recovery after environmental disturbances (Ayuso et al. 2016, Faist et al. 2020). Abed and colleagues (2014) used chlorophyll analyses to investigate the correlation between cyanobacteria hydrotaxis and the rapid biocrust greening on wetting. By using high-performance liquid chromatographic and hyperspectral imaging, the researchers concluded that Chla concentration increased after wetting only at the top layer, whereas its vertical profile did not change. Furthermore, ¹³C-labeling experiments demonstrated that the greening on wetting was not due to *de novo* synthesis of Chla, but rather to the rapid recovery of the pigment already present in the biocrust. Overall, the photosynthetic apparatus remains essentially intact and return to a functional state with remarkable speed. In addition, cyanobacteria did not exhibit any hydrostatic movement to track water but, instead, increased their Chla production and restored their photosynthetic activities within minutes of water addition. Román and colleagues (2019) demonstrated that biocrust reflectance provides a nondestructive and reliable method to quantify Chla and, therefore, to study the biocrust state and development. Recently, the Chla absorption feature in the red region was recognized as a robust and sensitive index of biocrust greening being minimally affected by the soil moisture content. The index was then applied to the optical images obtained from the satellite Sentinel-2 and proved to be suitable for tracking the spatial and temporal development of biocrust along the rainfall gradient in the Negev Desert (Panigada et al. 2019).

Because colored SAB are usually observed on stone heritage (box 2), the content of photosynthetic pigments has been widely used to estimate the phototrophic biomass colonizing construction materials and ornamental stones. For instance, Vázquez-Nion and colleagues (2018) measured Chl fluorescence (as a proxy of growth and physiological state) and color variation (as a proxy of biomass estimation and pigment production) to assess the primary bioreceptivity to phototrophic SABs of eleven varieties of granitic rocks. The color variation was measured by using the CIELAB color space coordinates that represent each color using three scalar parameters: L*, lightness or luminosity of color; a*, associated with changes in redness-greenness; and b*, associated with changes in yellowness-blueness. Vázquez-Nion and colleagues (2018) reported enhanced granite colonization rates on substrates with high open porosity, capillary water content, and surface roughness. The effects of substrate bioreceptivity and environmental parameters on SAB development were investigated by using the same pigment-based techniques: Chl fluorescence and color variation (Fuentes and Prieto 2021a). The study revealed that granite bioreceptivity affected microorganisms' adhesion to the substrate, water stress hindered biofilm formation,

and temperature promoted photosynthetic efficiency. Chl fluorescence measurements were also used to investigate the effects of water-induced stress on phototrophic SABs, where 2 days of drought were found to influence the vitality and recovery of the microorganisms (Fuentes and Prieto 2021b). Photosynthetic pigments content and color measurements revealed that high levels of atmospheric carbon dioxide favor the development of phototrophic SABs, although the effects of increased carbon dioxide levels were counteracted by increased water availability (Prieto et al. 2020).

The cyanobacteria-dominated endolithic colonization in halite deposits of the Atacama Desert hyperarid zone was investigated with λ -scan confocal laser scanning microscopy to detect autofluorescence emission spectra of photosynthetic pigments (Roldán et al. 2014). Photosynthetic pigments could be identified according to the shapes of the emission spectra and wavelengths of fluorescence peaks. Red fluorescence produced by Chla and phycobiliproteins was considered an indicator of cell viability. Once faded, a nonspecific green fluorescence appeared, either because of the variety of compounds (e.g., flavonoids and pyridine nucleotides) or because of the degradation of the photosynthetic pigments and the increasing amount of denatured proteins (Roldán et al. 2014). Therefore, photosynthetic pigment fingerprints emerged as indicators of cell viability that can be exploited to search for extraterrestrial life (box 3). The same technique was applied by Villa and colleagues (2020) to study the healthy state of phototrophs colonizing a stone monument before and after a cleaning treatment. The pigment spectral profile of SABs exposed to a chemical treatment showed characteristic emission peaks between 540 and 590 nm, indicating the disorganization of the light-harvesting complex.

To study the effects of increasing nitrogen inputs on biocrust structure and function, Dias and colleagues (2020) used the number of pigments and their relative abundance as a proxy for SAB richness and evenness, respectively. The results revealed that biocrust diversity—as is shown by pigment richness and evenness—increased with increased nitrogen inputs. Therefore, pigment-based data suggested that increased nitrogen inputs promoted biocrusts multifunctionality, which may be instrumental in counteracting the negative effects of climate change and desertification in drylands.

Toward microbial pigment ecology

Because pigment-based color is the hallmark of all SABs, it could be exploited to study the mechanisms driving changes in community structure and function under the influence of perturbations and microbial coexistence across different environments.

So far, we have presented pigment-based color as a trait that promotes adaptation for resource allocation and survival benefits and that reflects the physiology and activity of the SAB community. These concepts can also be seen in the framework of trait-based life-history strategies. Trait-based

life-history strategies simplify the complex trait information into a few ecologically relevant elements and simultaneously offer tools to characterize changes in community structure and function due to stress (persistent adverse climatic and environmental conditions) and disturbance (event leading to significant loss of biomass or rock surfaces rejuvenation, and surface instability).

Grime's (1977) CSR (for *competitor, stress tolerator, ruderal*) framework is a classic trait-based approach that classifies organisms responding to stress and disturbance. Although originally developed to explain plant-community assembly, the CSR theory can be applied to seek general patterns of microbial communities' organization (Villa et al. 2016, Wood et al. 2018). Therefore, it is possible to use the CSR framework to illustrate the interface between pigments and microbial life history (figure 2). According to the CSR theory, competitors thrive in low-stress and low-disturbance environments, where they gain a competitive advantage by maximizing resource acquisition. Competitive traits associated with pigments are related to the improvement of resource acquisition and the control against undesired neighbors. An interesting example of a competitive trait is provided by the brown pigment pulcherrimin, which is excreted by *Bacillus* and yeast species generally found on mineral substrates. From the chemical point of view, the pulcherrimin is a chelate complex of pulcherriminic acid and ferric ions. Iron is the most important metal in biology, and previous studies showed that external iron strongly influences biofilm formation in several microorganisms (Rizzi et al. 2018). Pulcherrimin manipulates the microenvironment of the biofilm through the depletion of iron (Arnaouteli et al. 2019). A partial depletion in high-iron conditions allows *Bacillus subtilis* to colonize a surface and gain access to nutrients. Furthermore, the presence of the iron-chelating pulcherrimin can prevent bacteria found in the surrounding environment to invade the biofilm through the generation of an iron-free zone (Arnaouteli et al. 2019). In the same way, fungal melanin is an excellent metal-binding compound, and its metal scavenging activity allows the bioabsorption of essential metals from rocks and other mineral niches (Oh et al. 2021), conferring a competitive advantage by enhancing the mineral use. The yellow fungal pigment xanthocillin binds copper, affects cellular copper content, and possesses significant metal-dependent antimicrobial properties (Raffa et al. 2021). In summary, microorganisms capable of synthesizing certain pigments deprive competing cells of important resources while antagonizing undesired neighbors.

Stress tolerators endure suboptimal environments by maintaining metabolic performance in unproductive niches, which increases the efficient use of resources in the long term. It is suggested that microorganisms can synthesize pigments in response to stressful conditions to improve long-term growth and survival strategies in extreme environments. For example, heavy melanization was associated with the survival of microcolonial fungi under desiccation. Microcolonial fungi are rock specialists

that lack sexual reproductive structures and that form compact melanized colonies on bare rock surfaces (Coleine et al. 2021). Gorbushina and colleagues (2008) observed the maintenance of protective carotenoid precursors and constitutive antioxidants such as melanin and mycosporines in dormant microcolonial fungi following fast drying. Fungal melanin increases the cell's ability to absorb and retain water as a protection against desiccation. Melanin is known for its hygroscopic character and strong association with water, which determines its electroconductive properties (Cordero and Casadevall 2017). In addition, melanization can change the strengths and rigidity of the cell wall by crosslinking with different macromolecules. Melanin can also act as an osmoregulator by reducing the size of pores in the cell wall (Plemenitaš et al. 2008). Therefore, melanin affects the osmolyte exchange by reducing water loss and increasing cellular turgor forces (Casadevall Arturo et al. 2017). Desiccation also affects the EPM by changing its structural rigidity or elasticity. Scytonemin, widely distributed in the EPM of cyanobacteria, seems to stabilize the matrix that would give a survival advantage for terrestrial cyanobacteria during drought (Gao 2017). To survive periods of depleting oxygen concentrations, some microorganisms use melanin as terminal electron acceptors for anaerobic respiration and also as electron shuttles during the respiration of iron(III) minerals (Turick et al. 2009). This unusual use of melanin pigments advantages microorganisms by enhancing metabolic versatility in response to changing environmental conditions and by accelerating the biogeochemical cycling of metals. An increase in carotenoid concentration promotes cells' resistance to freeze-thaw stress by regulating membrane fluidity, which promotes cell viability at low temperatures and facilitates the nutrient transport (Seel et al. 2020). Carotenoids also improve bacterial tolerance in cells on acute xenobiotic shocks (Chia et al. 2021). In addition, the accumulation of the pigment protects the proteins involved in recovery, thereby, reducing the energy costs of the repair (Leung et al. 2020). All SAB-dwelling cells use a variety of mechanisms to allocate limited resources according to their current needs in the environment. Under xeric conditions and starvation, heterotrophs can meet energy demands by using sunlight as an alternative energy source through a BChl-based reaction center or proton-pumping rhodopsin (Zeng et al. 2020). In addition, to survive the fluctuating environment, microorganisms integrate light signals to produce appropriate behavioral responses. For instance, some Haloarchaea use microbial rhodopsins to sense light and guide phototaxis in search of optimal environmental niches (Chuon et al. 2021). It has been shown that light signals activate specific cellular acclimation programs through photoreceptors, preparing biocrust-inhabiting cyanobacteria for impending dehydration (Oren et al. 2019). Because hydration or dehydration cycles are likely to affect inorganic carbon levels, cyanobacteria acclimate to this fluctuation via their inorganic carbon-concentrating mechanism. The results by Oren and colleagues (2021) showed that far-red-light-sensing

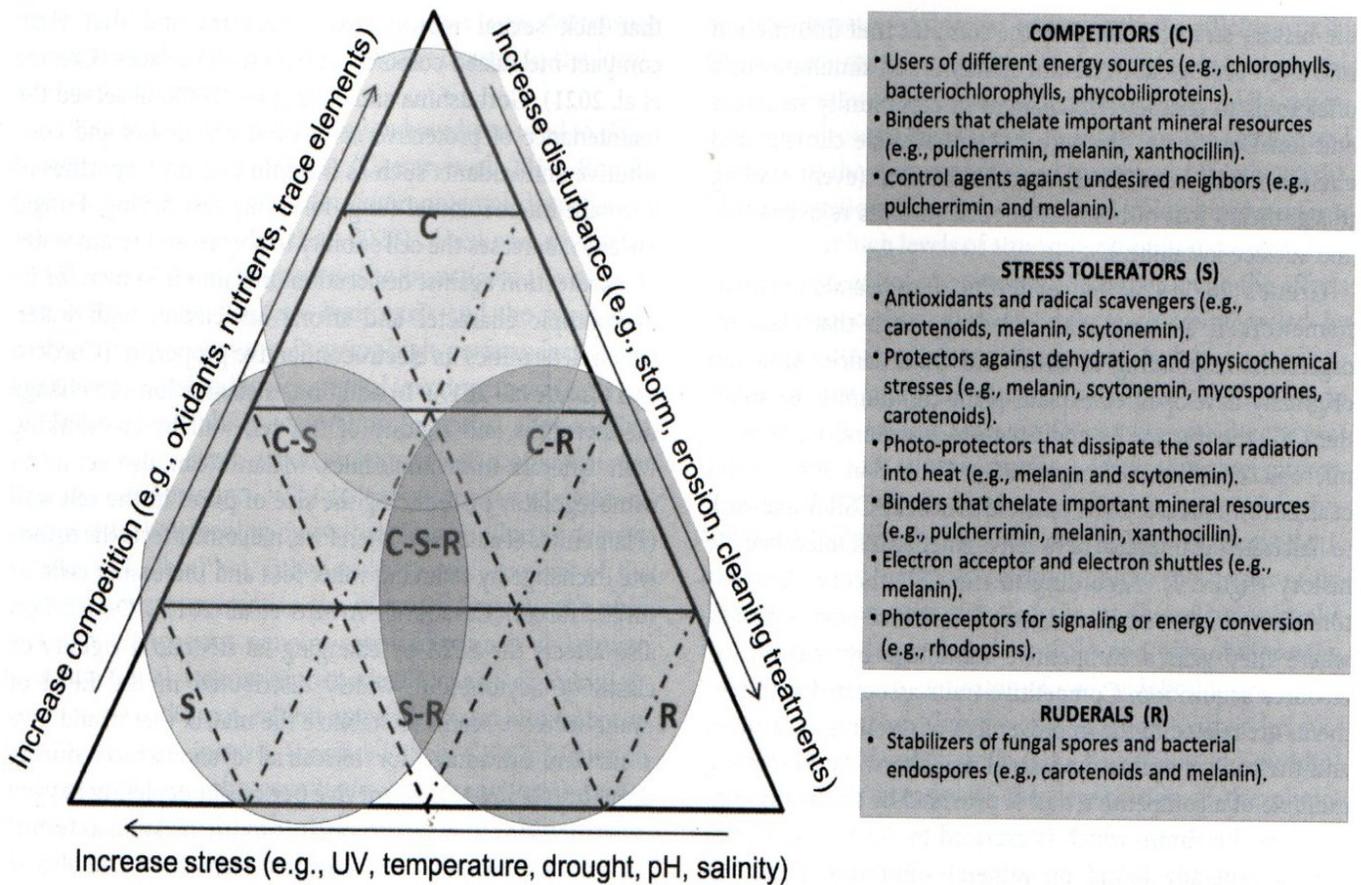


Figure 2. A reflection of pigmentation traits on the competitor (C)–ruderal (R)–stress tolerator (S) life strategy framework, as was proposed for plants by Grime (1977). The graphical representation combines the CSR context with resource acquisition and survival benefits for the microbial community.

photoreceptors—such as phytochromes—regulate the activity of the cyanobacterial carbon-concentrating mechanism, affecting desiccation tolerance in cyanobacteria. Overall, pigments provide SAB-dwelling cells with special properties that translate into survival and adaptation advantages during environmentally stressful conditions. Pigments can support the stress-tolerant strategy by serving as antioxidants and radical scavengers, protectors against dehydration and physicochemical stresses, photoprotectors that dissipate the solar radiation in the form of heat, binders that chelate important mineral resources, electron acceptor and electron shuttles, and photoreceptors for signaling or energy conversion.

Ruderals are microorganisms that cope with frequent disturbances by relying on high colonizing ability, rapid production of low-cost biomass, and inefficient resource uptake. The ruderal trait associated with pigments is the dispersal that is related to community recolonization. Some pigments confer advantages in ecological dispersion. For instance, the red pigment prodigiosin increases cell concentration in the aerosol produced by bursting bubbles (Syzdek 1985). Pigments are also involved in the development and stability of fungal spores and bacterial endospores. Studies demonstrated that pigment synthesis has provided an evolutionary advantage during sporulation, protecting the spores against harmful radiation (Moeller et al. 2005, Halaouli et al. 2006). We expect that microorganisms following ruderal strategies make less use of pigments than competitors or stress

tolerators because the disturbance might increase the risk of death before the pigment synthesis.

Pigments contribute to the differentiation of resource-use strategy with profound implications on the ecosystem structure and function. According to the coexistence theory, species should vary their use of resources (e.g., nutrients, water, light) to coexist in the same habitat. In other words, the more microorganisms vary in resource use, the greater the range of competitive abilities. Therefore, the presence of different pigments in a SAB community has consequences on the diversification of resource-use strategies, which enables different microorganisms to stably share a habitat, explaining—in part—the dazzling biodiversity of SABs. For instance, photosynthetic pigments cover the different regions of the solar light spectrum. The use of the light spectrum offers opportunities for niche differentiation and the coexistence of microorganisms with different light color absorbances (Stomp et al. 2004). A recent study carried out by Spaak and De Laender (2021) revealed that the combination of photosynthetic pigments in phytoplankton—a multispecies biofilm—is necessary for the species coexistence with a 40% increase in productivity compared with the single-pigment biofilm communities. Therefore, having such a wide range of pigments provides SAB communities enormous flexibility in tuning cellular responses to cues such as light and redox conditions.

Moreover, microorganisms sharing the same habitat can use pigments to different degrees (e.g., modulating levels

of the phycobilisome), and in pursuit of different resource strategies (e.g., promoting melanization that affects osmolytes exchange), leading to a redistribution of resource demand over space and time. In addition, pigments can drive facilitation (any interaction where the action of one microorganism benefits another) by boosting the growth of intrinsically less fit or more vulnerable microorganisms while relieving facilitators from the competitive pressure (Zélé et al. 2018). Wierzbos and colleagues (2015) observed a succession of organized colored horizons of algae and cyanobacteria within gypsum deposits in the Atacama Desert: orange algae cells close to the surface, green algae and cyanobacteria just below the orange layer, and a dark cyanobacterial layer at the bottom of the gypsum deposits in the hypoenolithic habitat (pore spaces in the undermost layer of the rock). The analyses revealed an enhancement of carotenoids and depletion of Chl in the orange cells in the cryptoendolithic habitat (pore spaces beneath the rock surface), suggesting that Chl-containing microorganisms took advantage of the protective carotenoids layer to escape from intense solar irradiation. The sunscreen pigment scytonemin was detected at the bottom of the gypsum deposits colonized by dark cyanobacteria. The compact and thick bottom layer of the gypcrete—generated by gypsum dissolution–recrystallization and water evaporation—has a high UV transmission rate that promoted the synthesis of scytonemin. Altogether, these results show that the spatial distribution of pigments can be linked to different colonization zones and microorganism types.

The differences in timing and speed of microbial responses to environmental fluctuations, including resource-use patterns, are found to underlie ecosystem resistance and resilience. Therefore, pigments may stabilize the SAB communities that are exposed to extreme events predicted to occur more frequently in the future. Overall, pigments may promote biodiversity, coexistence, and resilience through increased resource access, increased habitat heterogeneity, stress reduction, service sharing, and facilitation. These processes are expected to provide niche and fitness differences necessary to uncover the ecological mechanisms responsible for diversity–function relationships.

Outlook and future directions

Pigmentation is a ubiquitous trait among SAB-dwelling cells as it increases their fitness and plays a key role in the cells' life-history strategies. Although pigments are instrumental in supporting microbial life, there are clear gaps in our understanding of pigments' physiological function and SAB structure and activity that need to be filled. Many questions arise: the correlation between SAB features and pigment-based color, the physiological responses that are mediated by pigments, the change in pigmentation over time and through space, the genetics of pigment-based coloration, potential crosstalk and networks between pigment patterns and cell-to-cell communication, and the interplay between

pigmentation and biogeochemical processes such as nutrient cycling.

A major hurdle in the field of pigment ecology is the experimental determination of the pigments' physiological and ecological functions and their relationship with the SAB community. Unfortunately, most research on this topic has examined pigment functions by comparing non-pigmented and pigmented isolates or by studying the properties of purified pigments. Excluding other factors that are different between the strains or the use of non-physiological concentrations of the pigment might provide deeper insights that may more fully characterize the pigments' effects on the microbial phenotypes. Furthermore, despite our knowledge of the SABs' structure and function, we still do not fully understand the role of pigments in SAB ecology. The major issue relies on the different methods used until now to characterize SABs (microscopy, cultivation, omics), which make comparisons between data of different articles quite challenging to interpret. Therefore, standardized investigations are needed to untangle complex pigment–SAB relationships observed in the field. Recently, Lee and colleagues (2021) developed an automated sorting platform that separates the individual cell from the microbial communities on the basis of their Raman spectra. Sorted cells can be further analyzed by single-cell omics, coupling the phenotypic observation of the pigments to the molecular characterization of SAB-dwelling cells.

Multi-omics approaches are revolutionizing the way we study the structure and function of SAB communities. However, these molecular investigations required expensive equipment and qualified workers to execute the analyses and process the data. By contrast, color measurements (e.g., portable spectrophotometers) are simple, cheap, noninvasive, and not destructive. The groundbreaking idea would be to create a database where to collect multidisciplinary data sets including molecular, pigments, and color data. Then, data-analysis techniques and predictive algorithms can be applied to establish the correlation patterns between color profiles and SAB features. In this way, researchers and stakeholders can simply measure the SAB's color, and from this analysis infer the composition and activity of the microbial community at the mineral–air interface (figure 3). If we can use pigment-based color to predict SAB composition or behavior under different scenarios, we can better manage microbial adaptation to anticipate climate change, habitat loss, invasive species, or emerging infectious diseases. For instance, the contribution of microbial pigmentation in heat and water absorption is relevant not only for studying geographical patterns of SAB communities but also for estimating heat flow and physiological performance after a perturbation. Again, pigmentation may also help in answering important questions surrounding SAB ecology such as the shaping of ecosystems by microbial communities via color-mediated processes. Color can also indicate the effect of ongoing climate changes on microbial communities. For instance, the production of dark pigments is an ancient

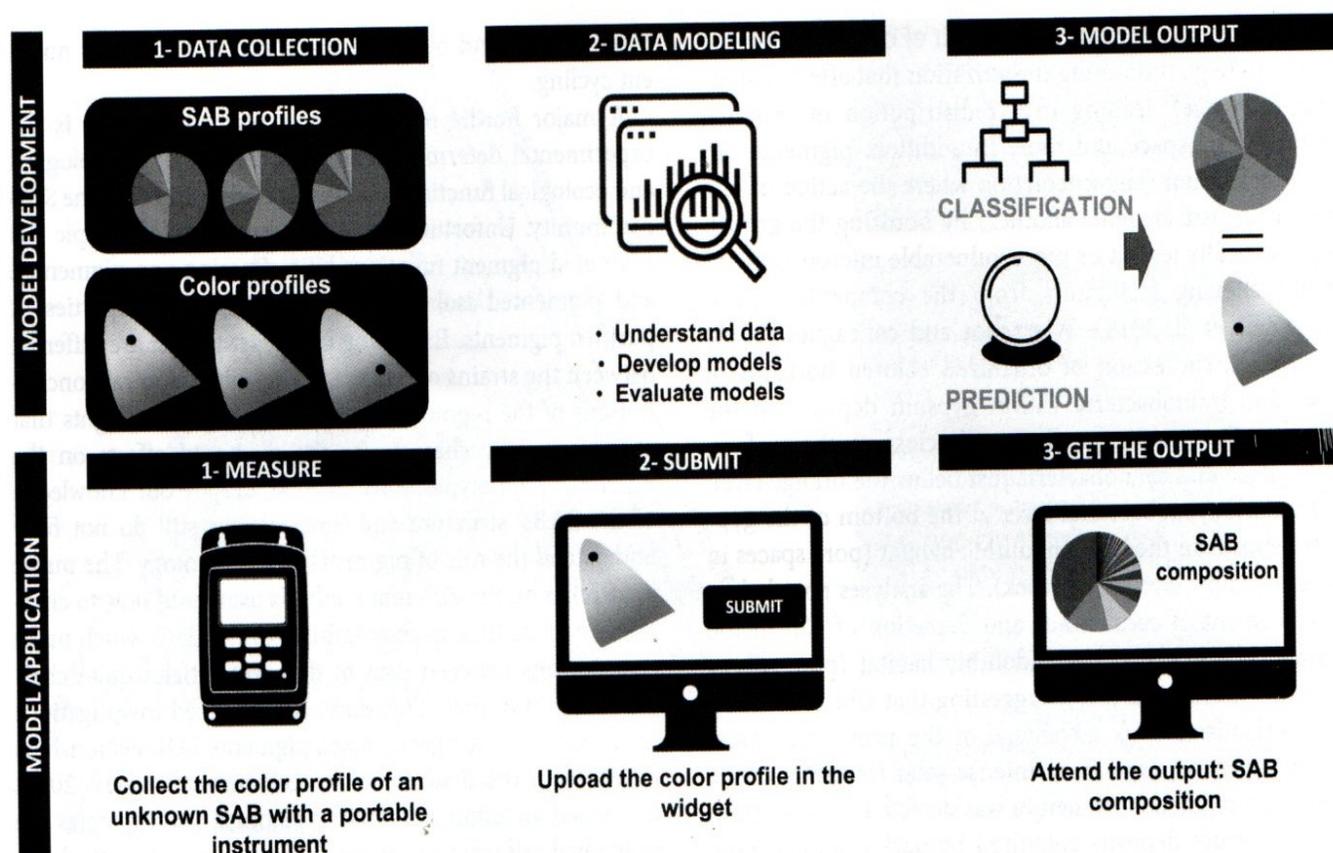


Figure 3. Use of color profiles to predict SAB community structure. Data-analysis techniques and predictive algorithms can be applied to establish the correlation patterns between color profiles and SAB composition. Researchers and stakeholders can simply measure the SAB's color, and from this analysis infer the composition of the SAB community.

adaptation mechanism for obtaining heat from solar radiation and could be an important variable in modeling climate change. SABs in colder climates darken themselves to capture more heat from the sun and improve their ability to survive (Cordero et al. 2018). These results suggest that dark pigmentation could help to predict whether a microorganism can survive at a given latitude as temperatures increase. However, dark pigmentation not only responds to climate change but also enhances it. As these dark pigmented SABs developed, they may set up a positive reinforcing loop in which the colonized area becomes warmer, speeding the glacial melt. There is already evidence that as glaciers melt, dark microbial colonies bloom in the meltwater (Azzoni et al. 2016).

The diverse structures and multifaceted roles of pigments make these molecules attractive targets for synthetic biology. The current trend is to use light to control biological circuits at the transcription level and to exploit wavelength-sensitive proteins. Bacterial behavior programming using light has shown great promise because of minimal toxicity and rapid activation or deactivation kinetics compared with chemical inducers. Therefore, it will be possible to regulate biosynthetic pathways or modify the structure and function of a SAB using a spectrum of individual light colors. Furthermore, there is a growing interest in engineering photosynthetic proteins as a component of biohybrid devices for solar energy conversion that is environmentally sustainable, efficient, and versatile. Recently, Liu and colleagues

(2020a) reported self-assembling chimeric photosystems, which employed a hybrid Chl-BChl solar energy conversion system for polychromatic solar energy harvesting and conversion. This approach was inspired by synthetic biology, where different pigments are exploited to create a programmable polychromatic photosystem. The photosystems are interesting materials for biohybrid devices with applications in photoelectrochemical solar energy conversion, fuel molecule synthesis, energy storage, biosensing, touch sensing, and photodetection.

The pigment-based ecology is a field that exemplifies modern research because it deals with a multifactorial phenomenon—pigmentation—that needs an interdisciplinary, technology-driven, multilevel, and integrative approach. Microbiologists, ecologists, biochemists, biophysics, and evolutionary biologists sharing a similar interest in pigmentation should come together to study the mechanisms of pigment production and perception, their intricacies of function, and their patterns of evolution. Mathematicians should incorporate these multidisciplinary data sets into new predictive models to test hypotheses about the role of SAB pigmentation (or SAB color) in biogeochemical cycles, biodeterioration versus bioprotection of stone heritage, ecosystem productivity, and climate change. The synergistic interplay among different disciplines will produce novel transformative ideas that will not only enrich our instinctive curiosity about colors but also provide a scientific basis for engineering SAB growth and obtaining colored

biomolecules for artistic and biotechnological applications. Interdisciplinary studies of the functional attributes of pigments at the mineral–air interface will promote the development of novel bioindicators for land degradation and desertification based on the color profiles of rocks and soil crusts' SABs. We are at the frontier of a new era in color science, and the interdisciplinary nature of this collaborative enterprise holds enormous promise for tackling today's global challenges, such as the management of natural and human-made ecosystems and the mitigation of climate change.

Acknowledgments

This contribution was supported by the CHROMA Project (SEED 2019 grant from the University of Milano no. RV_PSR_SEED_2019AZERB). The authors thank Professor Stefania Villa for providing the chemical structures of the main SAB's pigments. The authors thank Pancasatya Agastra Kusnandar for the English editing.

References cited

- Abed RMM, Polerecky L, Al-Habshi A, Oetjen J, Strous M, Beer D de. 2014. Rapid recovery of cyanobacterial pigments in desiccated biological soil crusts following addition of water. *PLOS ONE* 9: e112372.
- Adir N, Bar-Zvi S, Harris D. 2020. The amazing phycobilisome. *Biochimica et Biophysica Acta Bioenergetics* 1861: 148047.
- Antonaru LA, Cardona T, Larkum AWD, Nürnberg DJ. 2020. Global distribution of a chlorophyll *f* cyanobacterial marker. *ISME Journal* 14: 2275–2287.
- Arnaouteli S, Matoz-Fernandez DA, Porter M, Kalamara M, Abbott J, MacPhee CE, Davidson FA, Stanley-Wall NR. 2019. Pulcherrimin formation controls growth arrest of the *Bacillus subtilis* biofilm. *Proceedings of the National Academy of Sciences* 116: 13553–13562.
- Ayuso SV, Silva AG, Nelson C, Barger NN, Garcia-Pichel F. 2016. Microbial nursery production of high-quality biological soil crust biomass for restoration of degraded dryland soils. *Applied and Environmental Microbiology* 83: e02179–16.
- Azzoni RS, Senese A, Zerboni A, Maugeri M, Smiraglia C, Diolaiuti GA. 2016. Estimating ice albedo from fine debris cover quantified by a semi-automatic method: The case study of Forni Glacier, Italian Alps. *Cryosphere* 10: 665–679.
- Bartoli F, Ellwood NTW, Bruno L, Ceschin S, Rugnini L, Caneva G. 2019. Ecological and taxonomic characterisation of *Trentepohliaumbrina* (Kützing) Bornet growing on stone surfaces in Lazio (Italy). *Annals of Microbiology* 69: 1059–1070.
- Behrendt L, Breyndt A, Schliep M, Sørensen SJ, Larkum AWD, Kühl M. 2015. Chlorophyll *f*-driven photosynthesis in a cavernous cyanobacterium. *ISME Journal* 9: 2108–2111.
- Bhaya D. 2016. In the limelight: Photoreceptors in cyanobacteria. *Mbio* 7: e00741–16.
- Bowker MA, Reed SC, Belnap J, Phillips SL. 2002. Temporal variation in community composition, pigmentation, and Fv/Fm of desert cyanobacterial soil crusts. *Microbial Ecology* 43: 13–25.
- Brantley SL, Goldhaber MB, Ragnarsdottir KV. 2007. Crossing disciplines and scales to understand the critical zone. *Elements* 3: 307–314.
- Bryant DAY. 1982. Phycoerythrocyanin and phycoerythrin: Properties and occurrence in Cyanobacteria. *Microbiology* 128: 835–844.
- Caesar J, Tamm A, Ruckteschler N, Leifke AL, Weber B. 2018. Revisiting chlorophyll extraction methods in biological soil crusts: Methodology for determination of chlorophyll *a* and chlorophyll *a + b* as compared to previous methods. *Biogeosciences* 15: 1415–1424.
- Cappitelli F, Abbruscato P, Foladori P, Zanardini E, Ranalli G, Principi P, Villa F, Polo A, Sorlini C. 2009. Detection and elimination of cyanobacteria from frescoes: The case of the St. Brizio Chapel (Orvieto Cathedral, Italy). *Microbial Ecology* 57: 633–639.
- Cappitelli F, Salvadori O, Albanese D, Villa F, Sorlini C. 2012. Cyanobacteria cause black staining of the National Museum of the American Indian building, Washington, DC, USA. *Biofouling* 28: 257–266.
- Casadevall Arturo, Cordero Radames JB, Bryan Ruth, Nosanchuk Joshua, Dadachova Ekaterina, Heitman Joseph, Gow Neil AR. 2017. Melanin, radiation, and energy transduction in Fungi. *Microbiology Spectrum* 5: FUNK-0037-2016.
- Celedón RS, Díaz LB. 2021. Natural pigments of bacterial origin and their possible biomedical applications. *Microorganisms* 9: 739.
- Chatragadda R, Dufossé L. 2021. Ecological and biotechnological aspects of pigmented microbes: A way forward in development of food and pharmaceutical grade pigments. *Microorganisms* 9: 637.
- Chew AGM, Bryant DA. 2007. Chlorophyll biosynthesis in bacteria: The origins of structural and functional diversity. *Annual Review of Microbiology* 61: 113–129.
- Chia GWN, Seviour T, Kjelleberg S, Hinks J. 2021. Carotenoids improve bacterial tolerance towards biobutanol through membrane stabilization. *Environmental Science: Nano* 8: 328–341.
- Chun K, Kim SY, Meas S, Shim J-G, Cho S-G, Kang K-W, Kim J-H, Cho H-S, Jung K-H. 2021. Assembly of natively synthesized dual chromophores into functional actinorhodopsin. *Frontiers in Microbiology* 12: 652328.
- Cojoc LR, Enache MI, Neagu SE, Lungulescu M, Setnescu R, Ruginescu R, Gomoiu I. 2019. Carotenoids produced by halophilic bacterial strains on mural paintings and laboratory conditions. *FEMS Microbiology Letters* 366: fnz243.
- Coleine C, Gevi F, Fanelli G, Onofri S, Timperio AM, Selbmann L. 2020. Specific adaptations are selected in opposite sun exposed Antarctic cryptoendolithic communities as revealed by untargeted metabolomics. *PLOS ONE* 15: e0233805.
- Coleine C, Stajich JE, de los Ríos A, Selbmann L. 2021. Beyond the extremes: Rocks as ultimate refuge for fungi in drylands. *Mycologia* 113: 108–133.
- Cordero RJ, Casadevall A. 2017. Functions of fungal melanin beyond virulence. *Fungal Biology Reviews* 31: 99–112.
- Cordero RJB, Robert V, Cardinali G, Arinze ES, Thon SM, Casadevall A. 2018. Impact of yeast pigmentation on heat capture and latitudinal distribution. *Current Biology* 28: 2657–2664.e3.
- Corrochano LM. 2019. Light in the fungal world: From photoreception to gene transcription and beyond. *Annual Review of Genetics* 53: 149–170.
- Couradeau E, Karaoz U, Lim HC, Nunes da Rocha U, Northen T, Brodie E, Garcia-Pichel F. 2016. Bacteria increase arid-land soil surface temperature through the production of sunscreens. *Nature Communications* 7: 10373.
- Csotonyi JT, Swiderski J, Stackebrandt E, Yurkov V. 2010. A new environment for aerobic anoxygenic phototrophic bacteria: Biological soil crusts. *Environmental Microbiology Reports* 2: 651–656.
- Cui X, Liu X-L, Shen G, Ma J, Husain F, Rocher D, Zumbege JE, Bryant DA, Summons RE. 2020. Niche expansion for phototrophic sulfur bacteria at the Proterozoic–Phanerozoic transition. *Proceedings of the National Academy of Sciences* 117: 17599–17606.
- Culka A, Jehlička J, Ascaso C, Artieda O, Casero CM, Wierzbos J. 2017. Raman microspectrometric study of pigments in melanized fungi from the hyperarid Atacama Desert gypsum crust. *Journal of Raman Spectroscopy* 48: 1487–1493.
- DasSarma S, Schwieterman EW. 2021. Early evolution of purple retinal pigments on Earth and implications for exoplanet biosignatures. *International Journal of Astrobiology* 20: 241–250.
- De Felice B, Pasquale V, Tancredi N, Scherillo S, Guida M. 2010. Genetic fingerprint of microorganisms associated with the deterioration of an historical tuff monument in Italy. *Journal of Genetics* 89: 253–257.
- Dias T, Crous CJ, Ochoa-Hueso R, Manrique E, Martins-Loução MA, Cruz C. 2020. Nitrogen inputs may improve soil biocrusts multifunctionality in dryland ecosystems. *Soil Biology and Biochemistry* 149: 107947.