frontiers | Frontiers in Astronomy and Space Sciences

TYPE Mini Review
PUBLISHED 09 November 2022
DOI 10.3389/fspas.2022.1052278

The grit crust: A poly-extremotolerant microbial community from the Atacama Desert as a model for astrobiology

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SPECIALTY SECTION
This article was submitted to Astrobiology, a section of the journal Frontiers in Astronomy and Space Sciences

RECEIVED 23 September 2022
ACCEPTED 26 October 2022
PUBLISHED 09 November 2022

CITATION
Jung P, Lehnert LW, Bendix J, Lentendu G, Grube M, Alfaro FD, Rio Cd, Gutiérrez Alvarado JL, van den Brink L and Lakatos M (2022), The grit crust: A poly-extremotolerant microbial community from the Atacama Desert as a model for astrobiology.
Front. Astron. Space Sci. 9:1052278.
doi: 10.3389/fspas.2022.1052278

The grit crust is a recently discovered, novel type of biocrust made of prokaryotic cyanobacteria, eukaryotic green algae, fungi, lichens and other microbes that grow around and within granitoid stone pebbles of about 6 mm diameter in the Coastal Range of the Atacama Desert, Chile. The microbial community is very well adapted towards the extreme conditions of the Atacama Desert, such as the highest irradiation of the planet, strong temperature amplitudes and steep wet-dry cycles. It also has several other striking features making this biocrust unique compared to biocrusts known from other arid biomes on Earth. It has already been shown that the grit crust mediates various bio-weathering activities in its natural habitat. These activities prime soil for higher organisms in a way that can be envisioned as a proxy for general processes shaping even extra-terrestrial landscapes. This mini-review highlights the potential of the grit crust as a model for astrobiology in terms of extra-terrestrial microbial colonization and biotechnological applications that support human colonization of planets.

KEYWORDS

grit crust, astrobiology, Atacama, Mars, cyanobacteria, lichens, green algae

10.3389/fspas.2022.1052278

Introduction

Terrestrial extremophile microorganisms have ever since inspired hypotheses about life strategies in extra-terrestrial environments, e.g., on Mars, and about their applications in biotechnology-driven space activities. Such extremophiles usually include several hetero- and chemoautotrophic bacteria, archaea and fungi as well as photoautotrophic cyanobacteria and eukaryotic algae (Liu et al., 2008; Beblo-Vranesevic et al., 2018; Sundarasami et al., 2019; Coleine and Delgado-Baquerizo, 2022). A specific aspect of extreme environments has frequently been overlooked in this context: the symbiotic lifestyle, which is perfectly exemplified by biological soil crusts (hereafter: biocrusts). Moreover, the close coexistence and interacting of the biocenosis in a confined space also supports the response to sudden abiotic environmental fluctuations or changes and gives the community overall better resilience through different physiological use and response to change. These symbiotic associations of microorganisms are mainly found in hot and cold deserts across the globe, where they are often the main biological component colonizing the soil's surface (Weber et al., 2022). Soil particles are aggregated through the presence and activity of this often extremo-tolerant biota that desiccates regularly. The resulting living crust mantels the ground's surface as a coherent layer. It was estimated that biocrusts cover about 12% of the Earth's terrestrial surface and about 30% of all dryland soils (Rodriguez-Caballero et al., 2018). In these extreme environments, the microbial consortium regularly faces long periods of desiccation, intense UV radiation, and severe nutrient and resource limitations (Belnap et al., 2008; Munzi et al., 2019).

To overcome environmental limitations biocrust organisms have developed several strategies such as extracellular polymeric substances (EPS) that help them to retain water (Mugnai et al., 2018), UV-protecting pigments such as scytonemin (Miralles et al., 2017) or specific compounds including sucrose and trehalose (Xin et al., 2015; Baubin et al., 2021) that minimize metabolic desiccation stress. Most of these strategies have not yet been fully explored, and a plethora of novel genes and metabolites is expected from biocrust-forming microorganisms from extreme environments which can be used to obtain a wide variety of products using biotechnological processes (Lakatos and Strieht, 2017). Cyanobacteria and green algae are already optimal candidates for present biotechnological application on Earth due to low needs for maintenance (Schweiger et al., 2022). Therefore, this micro-algal-based technology could also be part of regenerative life support systems in space.

Beside such applications, biocrust-forming microorganisms as early terrestrial microbial associations on Earth can also help to address ancient humanity's questions, such as whether we are alone or how and where did life appear and evolve? This again has to do with their extremo-tolerant character, and the early time of their origins or their ability to interact with each other. Cyanobacteria, for example, which evolved during the late Archaean (Sánchez-Baracaldo and Cardona, 2020), can be found in virtually any environment on Earth and in symbiosis with fungi (Rikkinen, 2015) and plants (Chang et al., 2019). These microorganisms evolved at a time where the atmospheric composition of our planet and radiation income of the Sun were different. The Archaean Earth was devoid of oxygen and enriched by greenhouse gases (Hessler et al., 2004) including an increased exposition to higher fluxes of UV-B (280–320 nm) and UV-C (200–280 nm) radiation (Cockell, 2002). However, cyanobacteria could not only cope with these conditions (Shih, 2015), they also supposedly led to the Great Oxygenation Event during which they changed Earth's atmosphere and became ancestral to all other eukaryotic photosynthetic organisms such as algae and plants (Sánchez-Baracaldo and Cardona, 2020). This implies that cyanobacteria (and other microorganisms) resemble concepts of simple life forms that have a high adaptation potential to extreme conditions. Thus, we imagine that relatable life forms might be expected beyond Earth even if the abiotic conditions differ. Whether they are alive or extinct, they have and they still left their footprints on Earth, and we can learn to interpret the pattern they left as biosignatures to support the search for life on other planets at least in the Solar System and particular on planets such as Mars. Cyanobacteria, for example, are well known for their ability to form stromatolites on shores and lakes ranging in height from millimeters to tens of meters and extending laterally from small lenses to aggregates of hundreds of kilometers wide as mineralized domes (Neilan et al., 2002). If cyanobacteria alone leave such landscape-dominating traces behind in aquatic environments over millennia, how pronounced must then their traces be when they are an integral part of biocrusts together with lichens, green algae and other microorganisms that cover 12% of the Earth's terrestrial surface?

Recently, a novel type of biocrust was discovered in the Atacama Desert, one of the world's oldest and driest deserts, covering most of its floor: the grit crust (Jung et al., 2020a). The grit crust's microbial community is unique amongst biocrusts found in all other arid parts of the world because cyanobacteria, eukaryotic green algae, lichens and specific fungi grow on, in, and around small granitoid quartz pebbles called grits (locally called "maicillo") of about 6 mm in diameter. These structures can be seen with naked eyes and cause a blackish, landscape filling pattern, on the otherwise bare ground. The Atacama Desert is extremely interesting in that sense as it resembles an environment close to what is expected to be found on other planetary bodies, such as Mars, in terms of bio-geochemistry, nutrient composition or topological similarities - or at least mimics particular characters (Navarro-González, et al., 2003; Schmidt, et al., 2018). This can be explained by the unique combination of its environmental extremes such as its long lasting history of hyper-aridity, the highest UV radiation levels on Earth, oxidizing soils and other factors that can be

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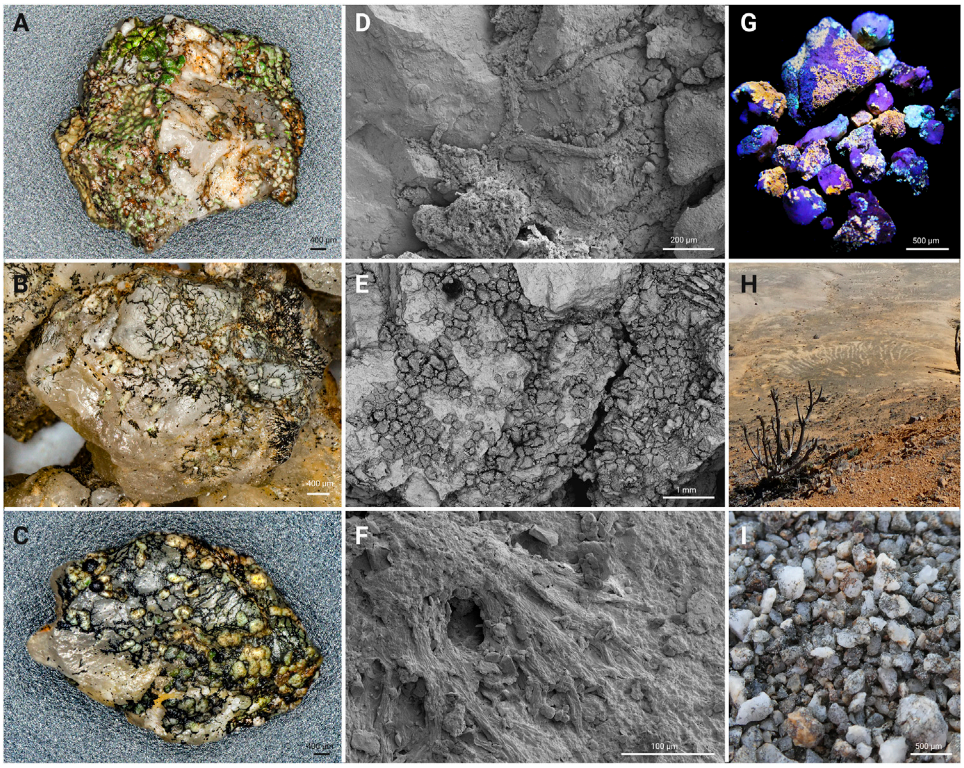

FIGURE 1
Potential fossilization traces of the grit crust depicted by various techniques. **(A–C)** micrographs of single grit stones in their hydrated state with lichens and fungi creating a vein-like network of micro-structures on the grit's surface. **(D–F)** scanning electron microscopy showing fungal trench lines in **(D)**, lichen squamules covered by mineral particles on grit stones in **(E)** and lichen pro-thallus in **(F)**. **(G–I)** photographs of the grit crust with glowing lichens in G caused by reflectance of secondary lichen substances under UV light, erosion rifts in **(H)** and a grit crust overview image with grits overgrown by various concatenating microorganisms in **(I)**.

compared with the conditions present on Mars (Azua-Bustos et al., 2022). For these reasons, an increasing number of experiments spanning from testing technologies over to experiments in the life sciences have been conducted at the Atacama Desert (Sobron et al., 2012; Abarca et al., 2013; Gunes-Lasnet et al., 2014; Schulze-Makuch et al., 2018). Thus, studying the survival and microbial diversity of the grit crust of the Atacama Desert during future studies will provide valuable insights into understanding the evolution of life, the habitability beyond Earth, and biotechnological applications of these microorganisms that could support space exploration missions.

Currently, the research project "Grit Life" funded by the German Research Foundation, aims to untangle the microbiota of the grit crust based on metabarcoding data applied to a recovery experiment over several years. This will not only give detailed insights into the diversity of bacteria, eukaryotes, and fungi but also tracks their re-colonization potential. The DNA-based approach is accompanied by monitoring climate and micro-climate data of the grit crust environment so that the extremophile character of the microbiota can be determined. In addition, fungi, eukaryotic green algae, and cyanobacteria of the grit crust will successively be isolated and curated in the context of a microbial archive in order to guarantee future investigations, e.g., on the microbe's biotechnological potential. As such, this project is the first of its kind that will generate a microbial archive of biocrusts where the extremophile properties of the microorganisms are characterized, allowing for transfer into biotechnological approaches. Exploiting this unique biocenosis will be discussed in the following in terms of the search for life beyond Earth based on novel potential fossilization structures known from the grit crust (Figure 1), and the utilization of the biocenosis' microorganisms for biotechnological approaches in space (Figure 2).

Suitability of the grit crust's ecology for the colonization of other planets

The grit crust covers a roughly 40 km broad strip, 2.5 km off the Coastal Range of the southern Atacama Desert (~26°S), spanning over 1.500 km to the northern Atacama Desert. In these areas, it forms blackish patterns on the desert's ground

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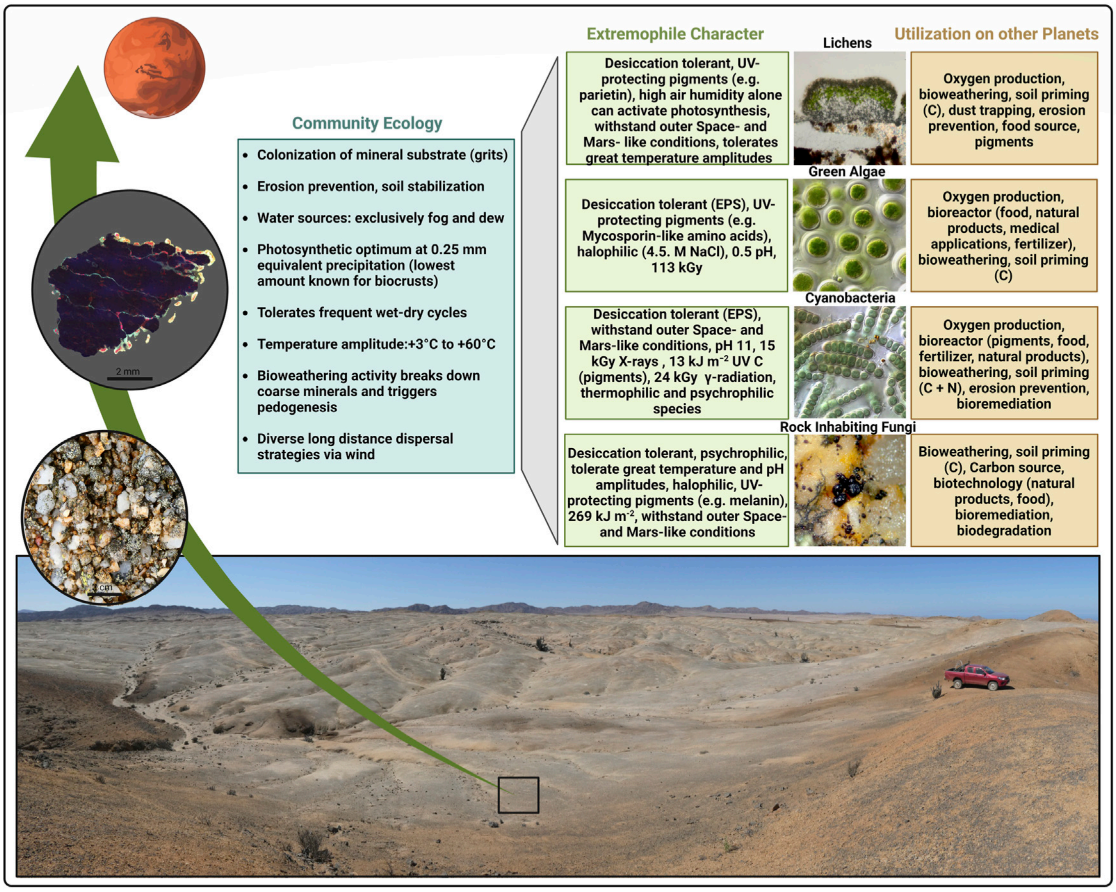

FIGURE 2
Ecology, extremophile character and possible applications of the grit crust in the context of astrobiology. The bottom picture shows the landscape of the coastal Atacama Desert with blackish patterns on the ground formed by a high microbial colonization degree. The bottom circle on the left shows a close-up photography of the ground with the grits colonized by diverse microbes such as lichens. The top circle shows a thin section of a single grit under the microscope using autofluorescence where fungal mycelium (lichens) appear whitish while algae appear red, which also colonize inner structures of the stone.

caused by a high degree of microbial colonization of the otherwise whitish granitoid quartz pebbles of approximately 6 mm diameter. These blackish patterns are so rich in organic material that they are well visible by the naked eye in the landscape. The reason for this is the cyclic appearance of fog and dew water input that leads to biomass growth equivalent to about 140 mg chlorophyll$_{a+b}$ m^{-2} and more (Jung et al., 2020a). These high biomass stocks are reached in a xeric environment where soil temperature can exceed 60 °C during summer days and falls below 3 °C during winter times. Average water input from dew is only 0.025–0.088 mm per day, water input from fog is 0.38–1.25 mm per day, and intense irradiation, with maxima of more than 1,500 µmol photons m^2 s^{-1} is frequent (Jung et al., 2020a). In general, the Atacama Desert is considered as a radiation hotspot where the highest irradiation on the planet was reported (Rondanelli et al., 2015). Constituents of the microbial community are diverse micro-lichens (*Buellia* spp., *Pleopsidium chlorophanum*, *Tetramelas pulverulentus*, *Aspicilia* spp., *Diploschistes* spp.), with green algal photobionts (*Trebouxia* spp., *Myrmecia* spp.), free living eukaryotic green algae (*Stichococcus* spp., *Pseudostichococcus* spp., *Chlorella* spp., *Klebsormidium* spp.) and cyanobacteria (*Nostoc* spp., *Microcoleus vaginatus*, *Kastovskya adunca*, *Myxacorys chilensis*, *Pleurocapsa* spp.), as well as melanized micro-colonial fungi (*Constantinomyces* spp., *Lichenothelia* spp.) (Jung et al., 2020a). These harsh conditions under which they thrive may indicate that the microbial community building the grit crust - or at least individual strains contained therein - might be suitable candidates for testing (their) vitality in outer Space or under Martian conditions (Coleine and Delgado-Baquerizo, 2022). Here, it is also worth to mention that unicellular life forms evolved early in the Earth's history. On the other hand, the climate of the Atacama Desert is considered to be stable for at least 150 million years (Hartley at al., 2005), which leads to the idea that the microbial life forms that jointly build the grit crust of the Atacama Desert are well adapted to extreme environments. Although other microbial consortia are known from hyper-arid regions of the Atacama Desert (e.g. Schulze-Makuch et al., 2018), the grit crust is exposed to low amounts of fog in areas devoid of any higher vegetation (Jung et al., 2020a) and it is the only microbial assemblage which fills entire landscapes of hundreds of square kilometers (Jung et al., 2020a). This demonstrates the ecophysiological adaptation potential of the grit crust on the large scale environment which might be beneficial for microbial colonization of other planets with relatable conditions.

Surviving prolonged desiccation is a common feature of all organisms mentioned here, but in addition, it has been shown that the photosynthetic activity of the grit crust is strongly inhibited when more than the equivalent of 0.25 mm water is present in the organisms (Jung et al., 2020a). This amount also marks the range in which the net photosynthesis of the microbial community is at its optimum. At the same time, this is the lowest amount of water for optimum photosynthesis detected for biocrusts on Earth (Jung et al., 2020a). Amongst biocrusts, the grit crust from the Atacama Desert is also unique in its adaptation to wet-dry cycles caused by several fog events during a single day because these cyclic conditions have been shown to be harmful for other biocrusts (Belnap et al., 2004; Reed et al., 2012). This implies that the grit crust's microbial community could be ideal for biotechnological applications outside its natural environment, such as humanly induced microbial colonization of other planets, where cyclic artificial wetting will for sure be essential, but in the case of the grit crust - compared to other biocrusts - not lethal due to their specialized desiccation tolerance.

One of the biggest challenges during human colonization of other planets has been the formation of soil as a weathering product of mainly unweathered rocks found on other planets. Access to nutrient rich soil would subsequently allow the growth of microorganisms and/or plants in order to support human life. The grit crust is the first biocrust detected on a pure mineral, coarse substrate, while most other biocrust types are established on soil, a product of a later stage in the weathering of minerals (Weber et al., 2022). This resembles another benefit of the grit crust compared with other biocrusts because coarse minerals are the predominant substrate found on, e.g., Mars and the Earth's moon. Mars' surface consists mostly of coarse regolith of largely weathered basalt (McSween et al., 2009), which contains the basic macro elements (C, H, O, N, P, S, K, Mg, Na, and Ca) and minor elements (Mn, Cr, Ni, Mo, Cu, Fe, and Zn) essential for life (Greenwood et al., 2007; Stern et al., 2015; Verseux et al., 2016). However, due to the lack of organic carbon, the basaltic regolith substrate has a poor water-holding capacity and limited nutritional bioavailability (Wamelink et al., 2014).

Despite colonization of the quartz pebbles' surface, the grit crust microorganisms also inhabit the undersurface and naturally occurring cracks where they are protected from harsh UV radiation but can still perform photosynthesis due to the transparent to translucent character of the stones. It has also been shown that these microorganisms actively mediate bio-weathering activities regarding nutrient acquisition, which can lead to the formation of a terrestrial protopedon as initial pedogenesis (Jung et al., 2020b). This terrestrial protopedon is a fine substrate enriched in nitrogen from cyanobacterial nitrogen fixation and carbon from photosynthesis that primes the substrate for the establishment of other organisms and leaches into deeper layers (Dojani et al., 2007; Young et al., 2022). Triggering this succession is a well-known feature of biocrusts worldwide (Belnap and Weber, 2013; Barger et al., 2016; Bao et al., 2019), but the grit crust is the only biocrust type on Earth where minerals are the starting material and not (the more weathered) sand or soil. At the same time, the leaked or extracellular polymeric substances (EPS) of cyanobacteria, for example, together with the filamentous nature of some algae, the lichens and fungi concatenate the first millimeters of the substrate that protects it from erosion by, e.g., wind (Chamizo et al., 2017). This leads to the idea that the grit crust might have the potential to enrich mineral substrates of other planets over the long term and protects it from strong wind erosion, which is crucial on some Solar System bodies, e.g. Mars, where wind speeds can be immense (White, 1979; Viúdez-Moreiras et al., 2019). However, such strong winds could also be beneficial for colonizing great landscapes on other planets by the grit crust organisms, as these winds produce a lot of dust that can be transported over wide distances (e.g., Ferri et al., 2003), on which microbes can hitchhike. The Martian atmosphere is full of dust, with loads that greatly fluctuate with the year's season (Toigo and Richardson, 2000), so aeolian transport, including microbes, is a likely scenario that could support the microbial colonization of other planets that support human life. In the Atacama Desert, for example, it has been shown that certain soil-borne microorganisms were transported more than 100 km off the coast towards the hyper-arid core of the Atacama (Azua-Bustos et al., 2019).

Microalgae, lichens and fungi of the grit crust as models for astrobiology

On Earth, phototrophic extremophiles have been found in hostile environments, such as hot and cold deserts, hot, acidic, or alkaline springs, caves, or Antarctic sub-glacial lakes considered as Earth analogs of Mars and the icy moons of Jupiter and Saturn (Martins et al., 2017; Coleine and Delgado-Baquerizo, 2022). One of the most interesting microalgae occupying various ecological niches of such extreme habitats is the prokaryotic cyanobacterial order Chroococcidiopsidales, which has been a focal point for astrobiology research. For specific strains of the genus Chroococcidiopsis *sensu lato*, for example, it has been shown that they tolerate at least 4 years of air-drying (Billi, 2009;

Fagliarone et al., 2017), up to 13 kJ m^{-2} of UV C radiation (Baqué et al., 2013), 15 kGy of X-rays (Billi et al., 2000) and 12 kGy of γ-radiation (Verseux et al., 2016; Verseux et al., 2017). They even have an enhanced radiation resistance, coping with 30 kJ m^{-2} of a simulated Martian UV flux (Cockell et al., 2005), 24 kGy of γ-radiation and 2 kGy of Fe ions (Verseux et al., 2016). In their dried state, these strains also survived 2.5 years of exposure to Mars and Space-like conditions (Billi, 2019). Also a comparative analysis of whole-genome sequences showed no increased variant numbers in the space-derivate compared to triplicates of the reference strain maintained on the ground (Napoli et al., 2022). Closely related species that also belong to the order Chroococcidiopsidales, such as *Aliterella chasmolithica* (Jung et al., 2020c) and *Gloeocapsopsis diffluens* (Jung et al., 2021) were found in the grit crust environment, and a relative of the latter has been shown to produce great amounts of trehalose (145 µg per mg dry weight) and sucrose (64 µg per mg dry weight) as desiccation protection along with copious amounts of EPS (Azua-Bustos et al., 2019). This implies that these organisms have strong capabilities to protect themselves from damage during prolonged desiccation periods, a great characteristic for exposure to Space-like conditions during travel or terraformation approaches. Although these results were achieved for several strains of the order Chroococcidiopsidales, they likely also apply to other cyanobacteria—especially if they were isolated from desert environments such as the grit crust, where most of these extreme conditions come together. In addition to Chroococcidiopsidales, other cyanobacteria such as *Pleurocapsa* spp., the endemic *Kastovskya adunca*, *Myxacorys chilensis* and several *Nostoc* species have been found to be part of the biocenosis of the grit crust (Jung et al., 2019) and are expected to possess similar desiccation resistance functions.

In contrast to the great insights on the survivability of prokaryotic cyanobacteria exposed to Space- or Mars-like conditions, little is known about these capabilities for eukaryotic green algae. One of the most notorious green algae is the spherical and highly abundant genus *Chlorella* which can adapt to a range of extreme and harsh terrestrial conditions (Krienitz et al., 2015). Members of this genus isolated from desert sand crusts can resist intense UV radiation and γ-rays (Treves et al., 2013). In contrast to cyanobacteria, experiments, where *Chlorella* from desert environments was exposed to a Mars-like near-space environment showed that they survived but got significantly damaged on a sub-cellular and physiological level (Wang et al., 2021). We already detected several *Chlorella* and *Chlorella*-like types as frequent constituents of the grit crust, including *Pseudochlorella* spp. or *Pseudostichococcus* spp. which share similar characteristics. However, *Chlorella* is already used in large-scale bioreactors on Earth for commercial interests due to its ability to quickly adapt to cultivation conditions, because of the significant amounts of biomass generated in a short time, its CO_2 capturing ability and role as a food source (Coronado-Reyes et al., 2020). For these reasons, there are various ideas and concepts that suggest such green algae to be an integral part of lunar bases (Detrel, 2021) or on space stations (Helisch et al., 2016; Niederwieser et al., 2018), where a photobioreactor volume of 482 L has been shown to be suitable to ensure a daily CO_2 reprocessing for one crew member (Helisch et al., 2020).

Another component of the grit crust from the Coastal Range of the Atacama Desert are lichens, which -in general- represent a micro-ecosystem built by a fungus and an algal photobiont partner, including a vast microbiome (Hawksworth and Grube, 2020). Several lichen species have already been detected in the grit crust belonging to the genera *Aspicilia*, *Buellia* and *Pleopsidium* (Jung et al., 2020a), including some micro-colonial fungi of the genera *Lichenothelia* and *Constantinomyces* that are poly-extremotolerant (Gostinčar et al., 2012; Grube et al., 2013) and can facultatively be in symbiotic relationship with free-living eukaryotic green algae (Muggia et al., 2013). The lichen *Pleopsidium chlorophanum*, also present in the grit crust, was exposed uninterruptedly to simulated conditions of protected Martian surface niche conditions (269 kJ m^{-2}) for 34 days. The lichen not only survived and remained photosynthetically active but even adapted physiologically by increasing its photosynthetic activity over 34 days (de Vera et al., 2014). Similar results have been achieved for numerous other lichens (de Vera, 2012; Meeßen et al., 2013; Brandt et al., 2015; De la Torre Noetzel et al., 2017). In addition, black micro-colonial fungi (MCF), also referred to as rock-inhabiting fungi (RIF) (Sterflinger, 1998; Gorbushina, 2003), can cope with extremes of temperatures, acidity, osmotic stress and salinity, dehydration, solar and UV radiation and even radioactivity (Sterflinger 1998; Gorbushina, 2003; Onofri et al., 2007), with some of them being able to survive even real space exposure and simulated Martian conditions (Onofri et al., 2007). This indicates that lichens, their photobionts and RIFs as extremophile organisms, in general, can be great indicators to determine and prime the habitability of a planet and for the search of possible life-supporting surroundings on planets like Mars (Armstrong, 2019; Joseph et al., 2020).

Not only the singular microbes of the grit crust represent promising candidates for astrobiology but also their ecology as a community can give new impulses: the grit crust creates unique micro- and macroscopic patterns that can potentially get fossilized over time and that have until now not been included in the search for life on other planets. Paying attention to these structures is crucial and can complement investigations of fossilized microbial structures on other bodies of the Solar System or exoplanets. The structures of the grit crust microbes such as lichen thalli and fungal- or algal filaments, for example, can trap mineral particles rich in calcium carbonate that can fossilize as a venous network

(Figures 1A–C). A similar pattern might be created by trench lines generated by fungi that etch the quartz surface (Figure 1D). The later is a consequence of bio-weathering activity which has already been shown for the grit crust (Jung et al., 2020b). In addition, water erosion based on occasional heavy rain events play a crucial role in the Atacama Desert (Alcayaga et al., 2022). As the organisms concatenate the mineral substrate, the grits can create small gutters where excess water runs off, forming a slightly wavy micro-topography (Figure 1H). These "waves" are quite stable due to high contents of calcium carbonate that concatenates the waves which can later be fossilized over time. These and other structures can be visualized by various techniques such as simple photography using the full light spectrum or UV-radiation, scanning electron microscopy or stereoscopic micrographs (Figure 1), all of which are common for space missions (Joseph et al., 2020).

Concluding remarks

The Coastal Range of the Atacama Desert has recently been identified as the home to an outstanding biocenosis called grit crust, with a tremendous potential for various aspects of astrobiology. The ecology of the grit crust, including its extremophile microbial constituents, are unique amongst biocrusts on Earth that can be beneficial for human colonization of other planets or rock bodies such as the Earth's Moon or Mars. The new research project Grit Life aims to untangle the full microbial biodiversity of this grit environment, including isolating prominent microorganisms that will support future research in the context of astrobiology and space sciences. During these studies, the grit crust's extremophiles can be used to test their suitability during mass cultivation in photobioreactors (food-, oxygen source for crewed missions), screenings for Chlorophyll f (allows photosynthesis of cyanobacteria in low light environments such as on other planets) and symbiotic interactions (expands the knowledge on ancient life forms). For these reasons, the grit crust as a consortium of various microorganisms on a mineral substrate opens up a new opportunity to test hypotheses and ideas in the context of astrobiology that surpasses other biocrusts known on Earth.

Author contributions

PJ prepared the first draft of the manuscript and the figures. All authors revised the manuscript and approved the final.

Funding

The project "Grit Life" is funded by the German Research Foundation (DFG) with the grant number JU 3228/1-1. ML was funded by the Ministry of Science and Health Rhineland-Palatinate (PhytoBioTech, 724-0116#2021/004-1501 15405) and by the Federal Ministry of Education and Research (W2V-Strategy2Value, 03WIR4502A). FA and CR were supported by FONDECYT-1220358 and FONDECYT-11200789 respectively, Agencia Nacional de Investigación y Desarrollo (ANID), Chile.

Acknowledgments

The authors want to thank CONAF (Corporación Nacional Forestal) for their help in the context of this research project and the kind contributions of the rangers. Images were prepared with the great help of Biorender.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

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