

Beyond the extremes: Rocks as ultimate refuge for fungi in drylands

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ABSTRACT

In an era of rapid climate change and expansion of desertification, the extremely harsh conditions of drylands are a true challenge for microbial life. Under drought conditions, where most life forms cannot survive, rocks represent the main refuge for life. Indeed, the endolithic habitat provides thermal buffering, physical stability, and protection against incident ultraviolet (UV) radiation and solar radiation and, to some extent, ensures water retention to microorganisms. The study of these highly specialized extreme-tolerant and extremophiles may provide tools for understanding microbial interactions and processes that allow them to keep their metabolic machinery active under conditions of dryness and oligotrophy that are typically incompatible with active life, up to the dry limits for life. Despite lithobiotic communities being studied all over the world, a comprehensive understanding of their ecology, evolution, and adaptation is still nascent. Herein, we survey the fungal component of these microbial ecosystems. We first provide an overview of the main defined groups (i.e., lichen-forming fungi, black fungi, and yeasts) of the most known and studied Antarctic endolithic communities that are almost the only life forms ensuring ecosystem functionality in the ice-free areas of the continent. For each group, we discuss their main traits and their diversity. Then, we focus on the fungal taxonomy and ecology of other worldwide endolithic communities. Finally, we highlight the utmost importance of a global rock survey in order to have a comprehensive view of the diversity, distribution, and functionality of these fungi in drylands, to obtain tools in desert area management, and as early alarm systems to climate change.

ARTICLE HISTORY

Received 26 June 2020
Accepted 27 August 2020

KEYWORDS

Antarctica; climate change; dry limits of life; drylands; endolithic communities; extreme environments; fungi; rocks

INTRODUCTION

Drylands are among the most fragile areas on the planet. There, small changes in rainfall or temperature can result in dramatic changes in ecology and impact human-associated use of these regions. Drylands cover more than 40% of the terrestrial land surface area, and arid and hyperarid regions cover 11% and 6%, respectively. Due to global warming, a continued and dramatic expansion of drylands up to 56% is expected by the end of the 21st century (Cherlet et al. 2018).

In drylands, functioning ecosystems and viable populations of organisms must obtain water and limited access can lead to desiccation. The threshold of organisms' requirement for water is the dry limit of life (Wierzychos et al. 2012). Despite the arid nature of these areas, global desert ecosystems contain an often underappreciated and highly diverse microbial population. Life in the most extremely moisture-limited areas is generally restricted to lithic refugia, such as the pore spaces of coarse-grained rocks or the fissures and cracks of siliceous rocks, constituting the microbial endolithic communities

(de los Ríos et al. 2014). Under environmental conditions typically incompatible with active life, microbial colonization on rock surface can avoid extreme environmental conditions and endolithic niches provide thermal buffering, physical stability, and protection against high ultraviolet (UV) and solar radiation and, most especially, ensure water retention.

In many cases, endolithic microorganisms are extremophiles living at the edge of biological potential and represent the sole microorganisms able to withstand some of the most extreme conditions on Earth. Endolithic microorganisms have been reported to date in all hot and cold deserts worldwide (FIG. 1), where they represent the prevailing life forms ensuring ecosystem functionality, but they have been also observed at high altitudes or in temperate areas.

Endolithic microbial communities primarily colonize sandstone rocks (orthoquartzite) but can also colonize other rock substrates, including carbonates (e.g., DiRuggiero et al. 2013; Crits-Christoph et al. 2016), gypsum (e.g., Wierzychos et al. 2015), gypsum crust (e.g., Wierzychos

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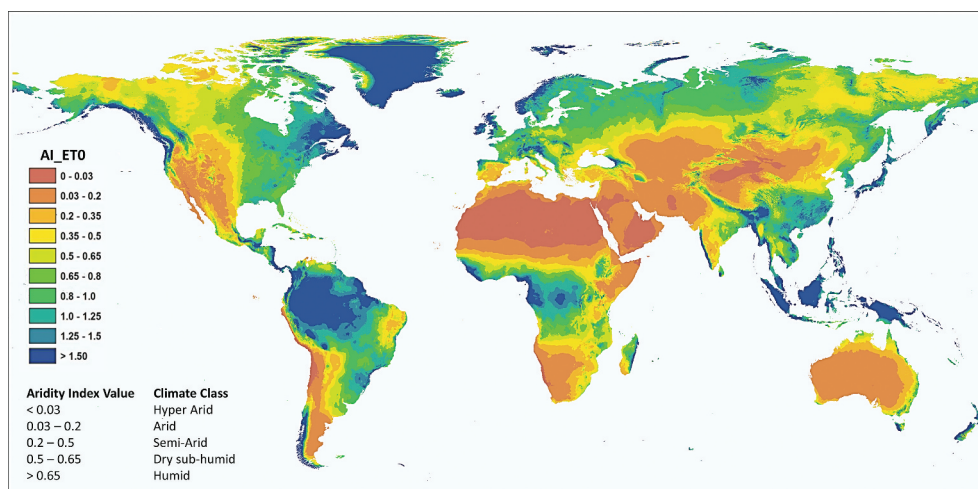


Figure 1. The Global Aridity Index (Global-Aridity_ET0) and Global Reference Evapotranspiration (Global-ET0) calculated for the entire globe (Antarctica is not included), available from Trabucco and Zomer (2018) at <https://doi.org/10.6084/m9.figshare.7504448.v3>. Higher AI_ET0 (green/blue colors) represents more humid conditions, with low AI_ET0 (brown/yellow colors) representing higher aridity. The United Nations Environmental Program (1997) breaks down the Aridity Index in the traditional classification scheme presented in the figure.

et al. 2011), halite (e.g., Gómez-Silva et al. 2019), and granite (e.g., de los Ríos et al. 2005b; Selbmann et al. 2017). The wide range of rock typology supporting endolithic life shows the versatility of these microorganisms to colonize different substrates and their notable ability to adapt to extreme environmental conditions. These rocky life forms are quite stable, due to the stable and protective nature of the endolithic niche where the microorganisms can live in strict spatial association with minerals; cryptoendolithism (i.e., ability to develop within natural pore spaces within the rock that are indirectly connected to the rock surface), chasmoendolithism (i.e., ability to grow in the natural fissures and cracks also connected to the rock surface), and euendolithism (i.e., ability to actively carve the rocks creating fissures and cracks connected to the surface) (FIG. 2) are the most predominant endolithic colonization modes.

Endolithic microbial communities are extremely simple in terms of biological diversity. Due to a relatively small reservoir of microorganisms that are highly specialized and capable to resist, develop, and adapt to rock endolithic microhabitats, Walker and Pace (2007) introduced the “metacommunity” concept. This concept supports the hypothesis that the endolithic microbial composition is consistent around the world. Endolithic communities are self-sustaining ecosystems, supporting a diversity of consumers, including both free-living and lichen-forming fungi, heterotrophic bacteria, and autotrophs represented by algae and cyanobacteria (Friedmann 1982; Omelon 2008; Wierchos et al. 2012), and consist of the most extreme-tolerant and extremophilic microorganisms known to date.

This pioneering research area started in the late 1960s, when I. Friedmann and R. Ocampo discovered endolithic communities in rocks from hot deserts; before then, no

one considered that life could exist within rocks. Nowadays, lithobiontic communities are being studied in deserts all over the world, since they are of importance in a wide variety of disciplines and excellent model systems for studying microbial interactions, to answer general questions in evolutionary ecology and adaptations necessary for the low complexity of microbial consortia. Endoliths play an important role in global biogeochemical processes; they contribute to the bioweathering and the structural and chemical alterations of rocks, as they are capable of numerous transformations of metals and minerals (Gadd 2007).

They are the main contributors in drylands to environmental/biogeochemical processes metabolizing C, N, and other macronutrients and mediate inputs and outputs of gases and nutrients and water uptake; they ensure the balance and functionality even in the harshest ecosystems, creating positive feedback for further colonization. Given their prominent contribution to dryland ecosystem functioning, information about their ecology and biogeography is of primary importance in order to prioritize ecosystem-level conservation and management efforts into preservation of dryland resources.

Endolithic communities are able to exist at limits of what is possible to support life on Earth. The study of these extreme microbial ecosystems can inform models and astrobiological studies investigating the habitability of extraterrestrial environments such as Mars (Cockell et al. 2016). The ability to colonize a wide variety of habitats, from relatively wet to extremely cold and dry, makes endoliths capable of acting as pioneers that can modify unsuitable substrates and uninhabited environments.

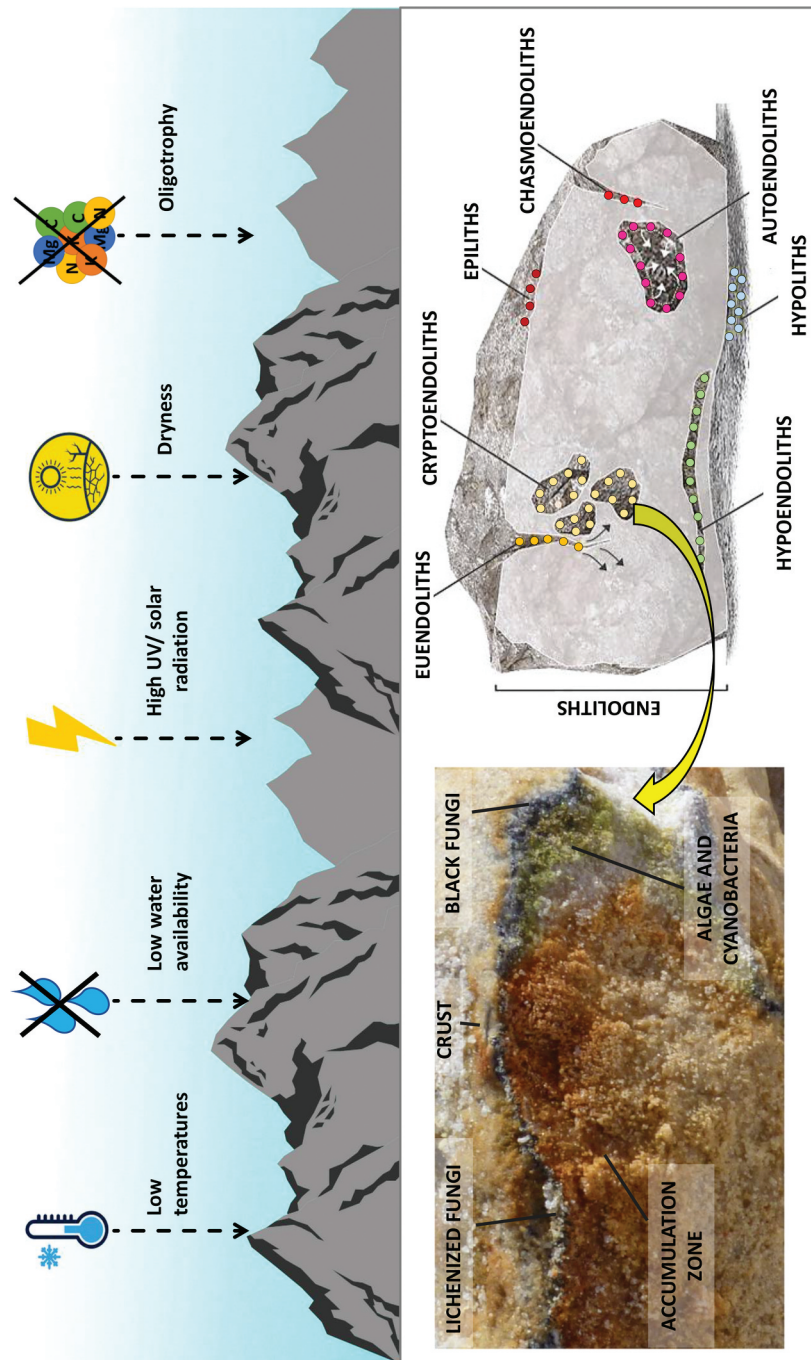


Figure 2. Rocks provide microbes with a refuge against external injuries such as low temperatures, temperature fluctuations, low water availability, oligotrophy, and harmful UV radiation. Bottom, right. Schematic representation of lithobionts redrawn from Amarelle et al. (2019). Epiliths (dark red dots) are located on the upper surface of the rock, whereas hypoliths (light blue) are found underneath the rock. Among endoliths, cryptoendoliths (light yellow) inhabit pores, chasmoendoliths (red) inhabit cracks or fissures, and hypoendoliths (light green) inhabit the lowest layer of the rock. Autoendoliths (fuchsia) can contribute to rock formation through mineral deposition, whereas euendoliths (orange) are those that actively penetrate the rock substratum. Bottom, left. A cryptoendolithic lichen-dominated community colonizing sandstone collected at Linnaeus Terrace (McMurdo Dry Valleys, southern Victoria Land, continental Antarctica) by L. Selbmann during the XXXI (Dec 2015–Jan 2016) Italian Antarctic Campaign. Photo credit: Italian National Program for Antarctic Researches (PNRA).

Thus, these microorganisms may represent analogues for Martian microorganisms. Blackhurst and collaborators (2005) speculating that if the endolithic microbial lifestyle has ever evolved on the Red Planet, it would be expected that a pioneering capability would lead to a strong selective advantage that would have been necessary for survival to more recent eras. It is, therefore, critical to further understand interactions between minerals and microorganisms in colonized terrestrial analogues in order to enhance the possibilities of identifying traces of past life in samples from extraterrestrial environments. In this context, the theory of “lithopanspermia” proposes the idea that life can be transferred from one planet to another through meteorites. This theory postulates that planetary bodies have been seeded with microorganisms that have colonized rocks that were expelled into space from life-harboring planets by asteroid impacts (Cockell 2008; Horneck et al. 2008). Although first documented in hot deserts, scientific interest in endolithic microorganisms increased after their discovery in the McMurdo Dry Valleys in southern Victoria Land (continental Antarctica), among the driest, coldest, and most remote places on Earth and believed to be devoid of life up until a few decades ago (Friedmann and Ocampo 1976). Whereas most of the Antarctic continent is covered with ice and snow, a tiny portion (less than 1%) is permanently ice-free and is mostly composed of exposed rocks and oligotrophic mineral soils (Ugolini and Bockheim 2008; Lee et al. 2017). There, the most abundant and well-studied endolithic communities are those dominated by lichens. Conversely, information from worldwide endolithic communities remains patchy still and is scattered or solely restricted to prokaryotes (e.g., see Wierzchos et al. [2012, 2015, 2018] and Meslier and Di Ruggiero [2019] and references therein) that have been regarded as the sole settlers to the harshest conditions, until recently (Horneck et al. 2016).

This review is focused on summarizing current research on Antarctic endolithic fungi, as they are pivotal organisms in endolithic communities. An initial description will be focused on the various roles of the substrate, highlighting rock properties critical for microbes, and on the environmental factors characterizing the Antarctic desert. In the second part, we will examine the state of knowledge on the ecology, taxonomy, and functional diversity of the main fungal components of endolithic communities (i.e., lichen-forming fungi, black meristematic fungi, and yeasts), pointing to the recent advances of new molecular-based research that has revolutionized the field of mycology. Finally, we will explore available data from worldwide fungal endolithic communities and revisit the “metacommunity” concept.

THE ROLE OF THE SUBSTRATE AND THE ENVIRONMENTAL CONSTRAINTS OF THE ANTARCTIC DESERT

The rock matrix: An oligotrophic substrate for fungal colonization.—Rocks represent a primary niche for microbial colonization in the harshest conditions of the ice-free area of continental Antarctica (see FIG. 3). Rock porosity, allowing the development of cryptic colonization, and translucence, facilitating photosynthetic activity and providing zonal growth a few millimeters below the rock surface, are key factors in the development and spreading of endolithic communities throughout high altitudes and long sea distances (Zucconi et al. 2016; Selbmann et al. 2017).

The physical structure of the substrate and the presence of minerals with high potential for water retention determine the hydration capabilities of the rock; indeed, highly diverse communities were associated with substrates that have high potential for water retention. The highly porous sedimentary rocks (e.g., the Beacon Supergroup sandstones of McMurdo Dry Valleys, southern Victoria Land) show a more homogeneous distribution of pores compared with other rock typologies. This sponge-like matrix facilitates water absorption and a tiny and uniform microbial growth; therefore, sandstone represents the most suitable niches for endolithic microbial colonization (Pointing and Belnap 2012; Selbmann et al. 2017). However, fissures and cracks of volcanic weathered siliceous rocks, such as granites, are also important reservoirs of endolithic colonization in other areas (de los Ríos et al. 2014).

Antarctic endolithic ecosystems are among the best available natural models for exploring organomineral interactions. Several analytical imaging and microscopy techniques (e.g., in situ microscopy) have been developed to provide a detailed description of living microorganisms and their relationships with the surrounding mineral substrates, identifying new-formed biogenetic minerals considered biomarkers of endolithic colonization (Wierzchos and Ascaso 1994; Ascaso et al. 1995; Ascaso and Wierzchos 2002; Wierzchos et al. 2003).

Physical factors influencing life in the Antarctic endolithic communities.—The microbial colonization of rocks is influenced by the rock substrate and additional abiotic factors (upper side of FIG. 3) (Omelon et al. 2006). Moreover, in such Antarctic environments, even minimal local variations in environmental conditions could be crucial for microbial life. A great deal of effort has been paid to elucidate how the combination of microclimatic, biological, and microstructural conditions shapes diversity patterns, community composition, and spatial distribution of these

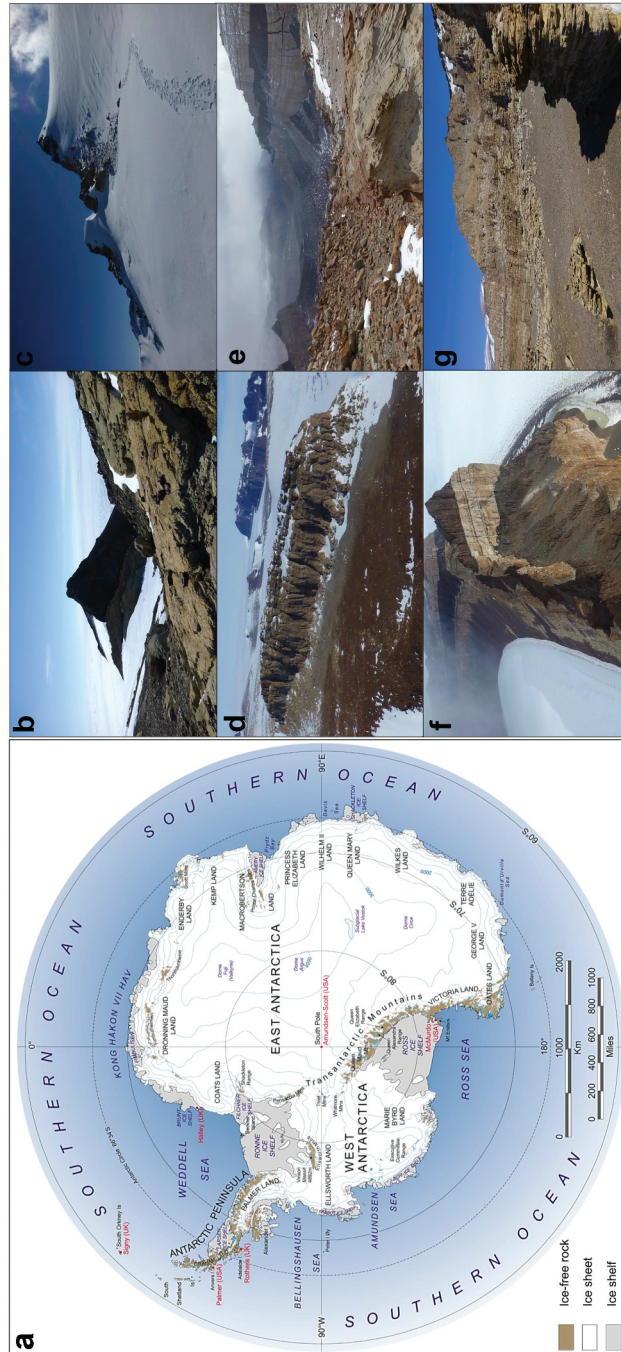


Figure 3. Localities visited along Victoria Land (continental Antarctica) during the XXXI Italian Antarctic Campaign. a. Map of the major geographic features of the Antarctic Continent produced by Landsat Image Mosaic of Antarctica (LIMA; <https://lima.usgs.gov/download.php>). It shows the topography of Antarctica, ice-free rock areas (in brown), ice shelves (in gray), and names of the major ocean water bodies (in blue uppercase text). b–d. Trio Nunatak, Mt. New Zealand, and Pudding Butte (northern Victoria Land). e–g. University Valley, Finger Mt., and Battleship Promontory (McMurdo Dry Valleys, southern Victoria Land). Photo credit: Italian National Program for Antarctic Researches (PNRA).

microbial ecosystems; together, these data may inform models and predictions on the impact of climate change.

Temperature. Low temperatures and, even more so, thermal fluctuations are among the most critical factors influencing success of lithobiontic microbial communities in Antarctica. Cold temperatures arrest metabolic activity (Friedmann and Weed 1987), and thermal fluctuations establish freeze-thaw cycles that contribute to the abiotic nature of rock surfaces.

Water. Water is fundamental for any biological process; therefore, its availability is the major limiting factor for active life in desert regions. Frozen water is biologically unavailable, and when temperatures are below the freezing point, which is the normal condition in Antarctica, the environment is water limited even when moisture is present. For this reason, even though more than 70% of the world's freshwater is located in the Antarctic plateau, the continent is considered the largest desert on Earth. Moreover, precipitation events are restricted to only a few snowfall events each year (Omelson et al. 2006), which are rare in the permanently ice-free areas of continental Antarctica. The thermal inertia of rocks permit the substratum to maintain heat from sun-exposed surfaces so that temperatures can be 20 C higher than the air temperature. Porous structures can retain liquid water and act as a sponge, enhancing the moisture content within rocks (McKay and Friedmann 1985; Vitek et al. 2016); this process leads to an increase of humidity within the rock up to 2-fold more than in the atmospheric air.

UV and solar radiation. Stratospheric ozone protects life on Earth from ultraviolet (UV) radiation; however, in Antarctica, UV radiation is substantially higher than elsewhere on Earth as a result of a depleted ozone layer (50% to 130% more UV radiation reaching the Earth's surface) (Madronich et al. 1998). The photosynthetically active region (PAR) is the zone within rocks inhabited by phototrophs defined by the depth light can travel through the substrate. The colonization is strongly influenced by the translucence properties and components of the host rock that can highly attenuate photosynthetically active radiation (PAR; 400–700 nm). Horath and coworkers (2006) found that the colonization zone was significantly deeper and wider in the sunlight-exposed rocks than in the shady surfaces. Microorganisms in the lichen-dominated cryptoendolithic communities are stratified according to their physiological requirements, and more light-sensitive phototrophs occur in the deeper

stratifications (Nienow and Friedmann 1993). In contrast, highly melanized fungi form a black band immediately beneath the rock crust, providing a screen for the whole community from direct exposure to harmful solar irradiation.

Other factors. Other factors such as wind, nutrient availability, and salinity also influence community composition. For instance, the lithobiontic lifestyle buffers against the effect of katabatic winds, which cause temperature fluctuations and erode the physical stability of the rock surface. Katabatic winds also determine a higher evaporation rate, leading to quicker water depletion and often leading to high concentrations of salts deposition on rocks and soil surfaces (Broady 1981). In the endolithic habitat, nutrients may be obtained from in situ weathered bedrock or allochthonous sediments, such as dust (Omelson et al. 2007). The suitability and microbial community makeup thereby depend on the local physicochemical properties of the colonized rocks.

How do endolithic microorganisms cope with stress?

Endolithic microorganisms survive harsh environmental conditions by finding refuge in rocks, occupying a niche that is uninhabitable for nearly all life forms, but also by displaying a wide array of microbial adaptive mechanisms (de los Ríos et al. 2014). One strategy is to limit metabolic activation to only for a few days per year when the temperature rises, snow melts, and humidity increases to levels that can allow microbial colonization (Friedmann and Ocampo 1976; Friedmann 1982). The ability of most endolithic microorganisms to enter a cryptobiotic state under poikilohydric conditions helps them to overcome the extremes without damage over long periods of otherwise lethal stresses.

Extracellular polymeric substances (EPS) are also a common feature of lithobiontic communities (de los Ríos et al. 2005b; Selbmann et al. 2005). These factors help maintain cellular structure, acting as a protective barrier and facilitating water retention and sorption of organic compounds and ions (de los Ríos et al. 2003; Omelson 2008). Endoliths produce UV-screening compounds such as scytonemin and carotenoids that can absorb radiation and inhibit UV-induced free radicals (Cockell et al. 2003; Vitek and Wierzbos 2020); they have also evolved special DNA repair mechanisms (Ruisi et al. 2007). The extreme desiccating conditions of arid and hyperarid areas have been the main driving force in the evolution of the DNA repair strategies that has generated the resistance, for instance, to ionizing radiation, which is a characteristic of several desert-derived microbes. Indeed,

desert regions represent a reservoir for new radioresistant taxa that have evolved special survival mechanisms, promoting adaptive radiation and speciation.

Overall, there is a limited understanding about the physiology and stress responses that allow these communities to maintain active metabolic machinery under conditions that are lethal for the most organisms. There have not yet been reports from metatranscriptome profiling to assess endolithic community gene expression, but this would be an important method to quantify the responses to temperature extremes and metabolism of these organisms. Future efforts should work to further establish the molecular basis of the functional traits of endoliths.

ADAPTATION OF LICHENS TO ENDOLITHIC NICHE

Overview.—Lichen symbioses are the most successful obligate symbiotic association of a heterotrophic fungal symbiont (usually Ascomycota) and a photoautotrophic partner (eukaryotic green alga and/or a cyanobacterium), facilitating their colonization with associated organisms throughout the harshest environments on Earth (Onofri et al. 2007). Lichens are placed in six classes of Pezizomycotina (Ascomycota), most are members of the Lecanoromycetes and the Arthoniomycetes (Grube and Wedin 2016). A smaller number of lichen-forming fungi are also members of the Basidiomycota. As lichens are self-sustaining ecosystems and may contain one or more photosynthetic partners and an indeterminate number of other microscopic organisms (including other fungi and bacteria), a more appropriate term of “lichen microbiome” has been coined (Cernava et al. 2017; Hawksworth and Grube 2020). Participants in the lichen consortium may adopt different lifestyles and diverse degrees of interrelationships; it has been proposed that an endolichenic lifestyle might represent an intermediate step between saprotrophic and endophytic lifestyles (Arnold et al. 2009; Naranjo-Ortiz and Gabaldón 2019). They are characterized by a unique and evolutionarily successful mode of survival to low water availability and long-term desiccation; they are dominant in several extremes, including polar regions and hot deserts (McKay et al. 2003; Wierzchos et al. 2012). They are well known as air pollution indicators around urban and industrial centers, and several efforts have been made to use lichens as monitors of climate change especially in cold regions; for instance, they are used as indicators of short-term climate oscillation in the Antarctic Peninsula (Sancho et al. 2019).

Ecology and taxonomy of Antarctic endolithic lichens.—Owing to their low mineral nutrient demand,

high freezing tolerance, anhydrobiotic behavior, and ability to be photosynthetically active at suboptimal temperatures (i.e., -5 to 20 C) (Kappen 2000; Bártak et al. 2007), lichens are considered exceptionally adapted to the lithobiontic lifestyle. Indeed, lichen-forming fungi are predominant in the Antarctic lichen-dominated cryptoendolithic communities (Friedmann 1982; Selbmann et al. 2017) and chasmoendolithic communities (de los Ríos et al. 2014), where the photobiont is mostly represented by the green alga *Trebouxia* (Chlorococcales) (Pérez-Ortega et al. 2012). Lichenized algae in these communities are considered the main source responsible for carbon fixation and sustain the entire community as primary producers.

Lichens can survive in the harshest conditions of the Antarctic desert not only by physiological adaptation to lower temperatures, but also by being able to grow penetrating through the rock porosity. However, a high proportion of dying and decayed cells are also integrated in Antarctic endolithic communities, which facilitates nutrient recycling (de los Ríos et al. 2004, 2005b). Long-term survival of endolithic lichens is linked to mineral-microbial interactions, which result in biogeophysical and biogeochemical alterations to the substrate and consequently formation of specific microenvironments (de los Ríos et al. 2005a, 2005b, 2014) (FIG. 4a–c). The unique adaptive achievement of Antarctic cryptoendolithic lichens is the ability of the mycobiont to change its growth from plectenchymatous to filamentous while still maintaining thallus organization with defined layers, and to revert to plectenchymatous when conditions allow epilithic growth. Lichens are involved in exfoliative weathering of laminar minerals and produce a significant amount of oxalic acid capable of dissolving the mineral cement of diverse rock types (Kappen et al. 1981; Jie and Blume 2002; de los Ríos et al. 2005a). Mergelov and colleagues (2018), analyzing endolithic systems from the bare bedrock surfaces in coastal oases of East Antarctica, demonstrated that transformation of silicate rocks by endolithic organisms is one of the possible pathways for the beginning of soils on Earth. Further comparative studies of the colonized and non-colonized rocks at the same sites may be an alternative method to distinguish the weathering induced by lichens from abiotic weathering mechanisms.

In the widest Antarctic rocks survey, performed up to 3600 m above sea level (a.s.l.) and from 0 to 100 km sea distance and samples analyzed by denaturing gel gradient electrophoresis, lichen-forming fungi (such as the two endemic species *Lecanora fuscobrunnea* and *Buellia frigida*, the heavily melanized *Umbilicaria* sp., and other undescribed species) were the most abundant in all typologies of rocks considered (e.g., sandstone, granite, dolerite) and

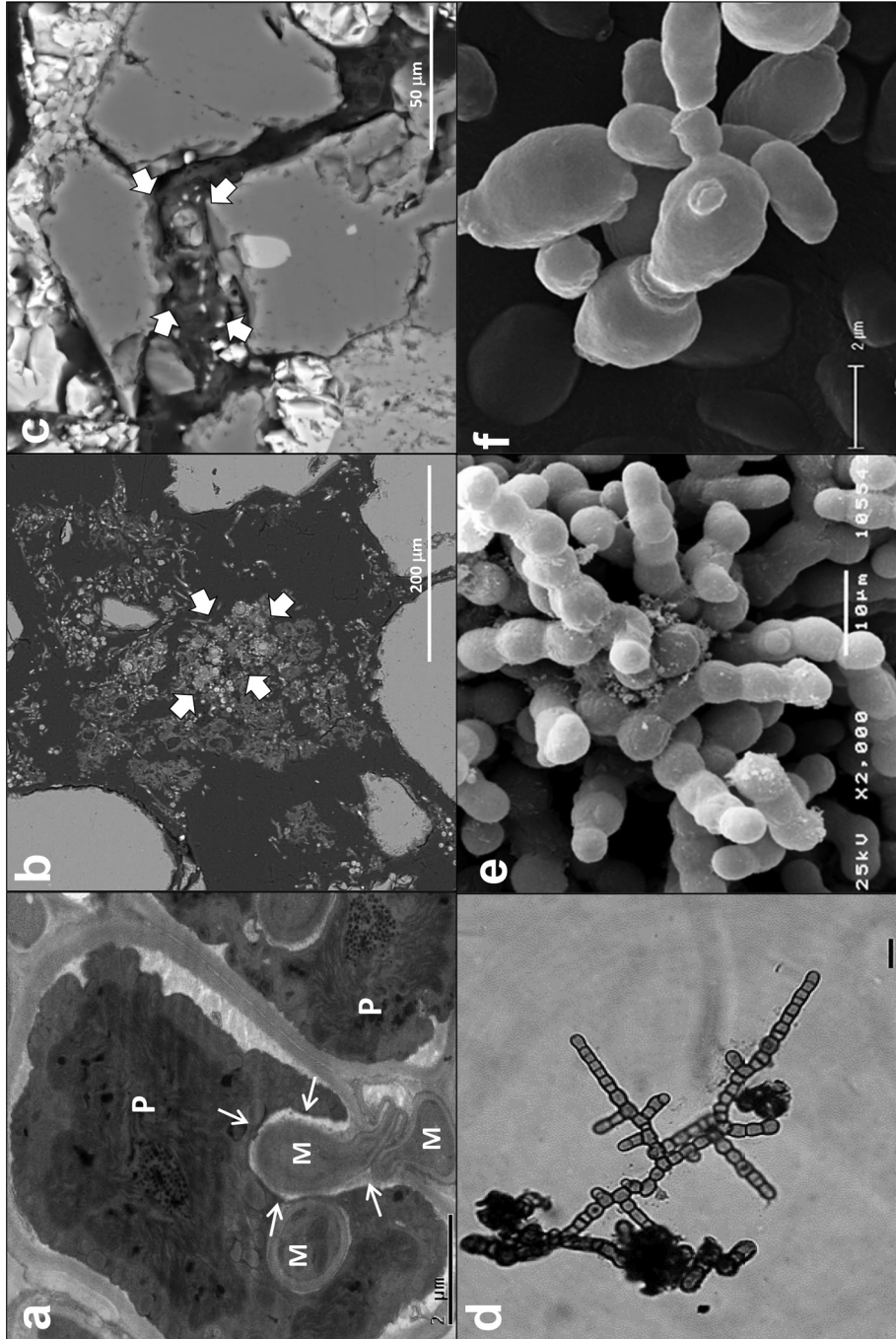


Figure 4. Microscope images of endolithic communities. a. Transmission electron microscopy (TEM) image showing the fungal-algal interface of *Lecidea* sp. symbionts; white arrows indicate the haustoria sheath; M = mycobiont, P = photobiont (de los Rios et al. 2005a). b. Scanning electron microscopy-backscattered electron (SEM-BSE) image of cryptoendlithic colonization in sandstones from University Valley (McMurdo Dry Valleys); arrows indicate endolithic lichen association. c. SEM-BSE image of chasmoendolith colonization in granites from Miers Valley (McMurdo Dry Valleys); arrows indicate endolithic lichen association. d. *Friedmanniomyces endolithicus* CCFEE 5208; light microscopy of moniloid hyphae and clumps of cells, with cells showing transverse septa. e. SEM image of *Cryomyces antarcticus* CCFEE 534; yeast-like organization and enteroblastic germination and seceded cells showing scars (Selbmann et al. 2005). f. SEM image of the strain *Taphrina antarctica* CCFEE 5198, cultured on malt extract agar after 3 weeks of incubation at 10 °C (Selbmann et al. 2014a).

their distribution spans to longer sea distances and higher altitudes (Selbmann et al. 2017). *B. frigida*, in particular, is a crustose endemic lichen widely found in both coastal and mountain locations across the continent (Jones et al. 2015). Recently, with the advent of next-generation sequencing methods such as pyrosequencing and metabarcoding, both prokaryotic and eukaryotic diversity have been characterized more deeply in these microbial ecosystems (Archer et al. 2017; Coleine et al. 2018a, 2019). The majority of fungal sequences obtained from Coleine and coworkers belonged to Lecanoromycetes as members of families Caliciaceae, Acarosporaceae, Lecideaceae, and Lecanoraceae, whereas three genera (*Buellia*, *Lecidea*, and *Acarospora*) were predominant and among “core” (i.e., species retrieved in at least 75% of analyzed samples) members of analyzed samples. Although these genera belong to different families, they show a remarkable morphological similarity in their cryptoendolithic growth form. Moreover, authors found that lichens were more abundant in northern sun-exposed rocks, and a few of them (Acarosporaceae, Caliciaceae, Catillariaceae, and Trapeliaceae) were identified as biomarker species for this condition (Coleine et al. 2018a, 2018b, 2020d). These findings supported the hypothesis expressed many years earlier for both hot and cold deserts (Friedmann 1977, 1978; Nash et al. 1977). According to these studies, lichen-forming fungi prevail in the northern-warm faces of the rocks, where higher temperatures make both melting of snow and metabolic activity possible. In contrast, the southern-shady rock surfaces, characterized by much more extreme conditions and more exposed to katabatic winds, are dominated by black microcolonial fungi.

Despite that endolithic lichens are extremely adapted and specialized to the harshest conditions of the Antarctic desert (few species are predominant in many rare taxa), they are highly resistant but scarcely resilient, resulting in high vulnerability, so they may be dramatically affected by any external perturbations, even those due to climate change (Selbmann et al. 2017; Coleine et al. 2018a, 2018b).

Although lichens are composite organisms and standard isolation procedures may fail, genomes of several lichen-forming fungi are now available. Recently, indeed, the role of hybridization as a potentially important mechanism for facilitating rapid speciation and adaptive radiations on lichen-forming fungi has been highlighted (Keuler et al. 2020).

Thus, we perceive the need to address future research efforts in developing optimized protocol to cultivate the mycobiont or using a metagenomic-like approach to reconstruct the genome sequences of Antarctic endolithic lichens, with a particular focus on clusters of genes involved in the stress

responses. Unraveling the relationship between genome features and environmental adaptation strategies is critical to understanding the ecological functions.

Antarctic endolithic lichens exposed to space-and Mars-imitated conditions.

Lichens are considered extreme-tolerant and extremophile microorganisms due to their ability to adapt and thrive in some of the most extreme environments on Earth (Rothschild and Mancinelli 2001). They are able to survive after immersion in liquid nitrogen (Kappen 2000) and as poikilohydric organisms (i.e., active when wet only); when inactive, they can tolerate extremes of light, temperature, and drought. For all these peculiarities, they have garnered the interest of astrobiologists and represent, nowadays, model organisms for astrobiological experiments (Sancho et al. 2007, 2008; de Vera et al. 2010, 2014). Antarctic saxicolous lichens have been successfully used in experiments under simulated space and Martian conditions (de la Torre et al. 2010; de Vera et al. 2003, 2004), and they have been launched in experiments at the International Space Station (ISS) such as the European Space Agency (ESA) LICHENS (Sancho et al. 2007) and Lithopanspermia (Sancho et al. 2008; Raggio et al. 2011) projects. Specifically, the LICHENS project aimed to determine, for the first time, the survival capability of lichens when exposed to space conditions; results indicate that most lichenized fungal and algal cells survived in space after full exposure to massive UV and cosmic radiation. The findings of this work could be correlated to the lithopanspermia theory, suggesting that life could survive an interplanetary transfer, from one planet to another (Cockell 2008; Horneck et al. 2008). In the framework of the ESA Biology and Mars Experiment (BIOMEX) project, the preflight test results indicate that *B. frigida*, growing on Antarctic rocks, was capable of survival within the simulated space conditions tested (Meeßen et al. 2015). After a duration of 1.5 years of exposure in low Earth orbit (LEO) and to Mars-like conditions, mortality substantially increased (Backhaus et al. 2019). In comparison with the results of the Lichens and Fungi Experiment (LIFE) project, which was performed using the cosmopolitan alpine lichen *Xanthoria elegans* (Brandt et al. 2015), the Antarctic endemic lichen *B. frigida* and its symbionts displayed a lower resistance to the severe space conditions. It has been hypothesized that *B. frigida* and its bionts, which colonize habitats characterized by severe environmental conditions, such as those found on continental Antarctica, present a lower resistance to the extreme conditions outside of the ISS than the worldwide distributed *Xanthoria elegans*, which was used in the LIFE project.

Cryptoendolithic Antarctic lichen-dominated communities were exposed to space for 1.5 years in the framework of the LIFE project (Onofri et al. 2012); once back on Earth, rock specimens were studied with culturomic approach and the lichen-forming fungus *Acarospora* sp. was isolated (Scalzi et al. 2012), informing on the possibility for eukaryotic life space transfer.

Certainly, further studies should be focused on adaptation processes operating within complex lichen symbioses to elucidate the limits of life strategies and the different levels among lichen species, depending on the environmental conditions of the respective habitats.

ROCK BLACK FUNGI REPRESENT THE EXCELLENCE IN THE HYPERARID AND COLD ANTARCTIC DESERT

Overview.—The terms “black fungi,” “black yeasts,” or “black meristematic fungi” (Sterflinger and Krumbein 1997) indicate a rather wide morphoecological group of fungi characterized for their strong melanization, ability to reproduce by unicellular growth, at least for a part of their life cycle, shift to a meristematic development, poor morphology, and very slow growth rate (de Hoog and Hermanides-Nijhof 1977; Sterflinger 2006) and that are exceptionally skilled in exploiting the extremes, including anthropogenic polluted environments (Selbmann et al. 2014b). The main unifying characteristic of black fungi is the accumulation of melanin, which acts as a protector against several chemical and physical stressors (FIG. 5a). Melanin can be also critical for the penetration of host tissue in plants and counteracts the oxidative stress of macrophages during the invasion of animal/human tissue, thus representing an important virulence factor, especially in Eurotiomycetes (e.g., *Exophiala dermatitidis*) (Xi et al. 2009; de Hoog et al. 2011). Outside of the host, melanin is a major contributing factor to the survival of black fungi, conferring extraordinary tolerance to chemical and physical stresses, including extreme pH, high and low temperatures, desiccation, ionizing radiation, and even alpha particles (Dadachova and Casadevall 2008; Gostinčar et al. 2011; Selbmann et al. 2011, 2018; Onofri et al. 2019), and important in the fungi’s capacity to resurrect from dry conditions (e.g., Gorbushina et al. 2008). In addition to melanins, these fungi tend to accumulate other protective compounds such as mycosporines, trehalose, polyalcohols, betaine, and carotenoids (Moreno et al. 2018).

Black fungi are highly adapted to diverse extreme environments and have been isolated from salt pans, hydrocarbon-contaminated sites, exposed bare rocks and monuments, icy habitats, deserts, solar panels, and building

roofs (e.g., Abdel-Hafez et al. 1994; Adams et al. 2006; Sterflinger et al. 2012; Ruibal et al. 2018; Perini et al. 2019).

Black fungi include rock specialists known as “micro-colonial fungi” (MCF) (Wollenzien et al. 1995) for which the term “rock-inhabiting fungi” (RIF) was more recently coined (Ruibal et al. 2009). RIF are peculiar organisms that apparently lack sexual reproductive structures and form compact, melanized colonies on bare rock surfaces (Sterflinger and Krumbein 1997). Although common, RIF are often overlooked due to their small size, extremely slow growth rate, and the lack of diagnostic features. Successful isolation of cultures requires a careful application of specific protocols (Urzi and De Leo 2001; Ruibal et al. 2005; Selbmann et al. 2014b); otherwise, cosmopolitan, fast-growing contaminants are unavoidably obtained (Gonçalves et al. 2016). First discovered in hot and cold deserts (Krumbein and Jens 1981; Friedmann 1982; Staley et al. 1982), RIF are now known to be ubiquitous on hard surfaces, in the far extreme as well as in more permissive climates (Sterflinger and Prillinger 2001; Gorbushina and Broughton 2009). RIF are adapted to oligotrophic and dry habitats where they are particularly successful due to limited microbial competition and their inherent tolerance to extreme environments.

RIF are phylogenetically quite diverse and comprise an assemblage of lineages mainly in two classes of the fungal kingdom: Dothideomycetes (orders Capnodiales, Pleosporales, Myriangiales, and Dothideales) and Eurotiomycetes (order Chaetothyriales). RIF in the class Arthoniomycetes have been reported from Antarctica and the Mediterranean but never formally described (Ruibal et al. 2009). Dothideomycetous RIF are overrepresented in cold, dry conditions, whereas specimens clustering in the class Eurotiomycetes, order Chaetothyriales, nearly exclusively thrive in hot, (semi-)arid climates, abundantly found colonizing marble monuments in the Mediterranean basin. These opposing distributions may be related to their distinct evolutionary origins. Using molecular-dating analyses, Gueidan et al. (2011) demonstrated that RIF in Dothideomycetes evolved in the late Devonian, and diversified during the Silurian–Devonian, about 430 million years ago, when large arid land masses prevailed and temperatures were much cooler than today. In contrast, Chaetothyrialean RIF originated in a period of recovery after the Permian–Triassic mass extinction and an expansion of arid land masses, about 250 million years ago, when global temperatures were relatively high. Dothideomycetous RIF are especially abundant rock inhabitants of the Antarctic desert.

Ecology and taxonomy of Antarctic endolithic black fungi.—RIF are also present in the Antarctic endolithic

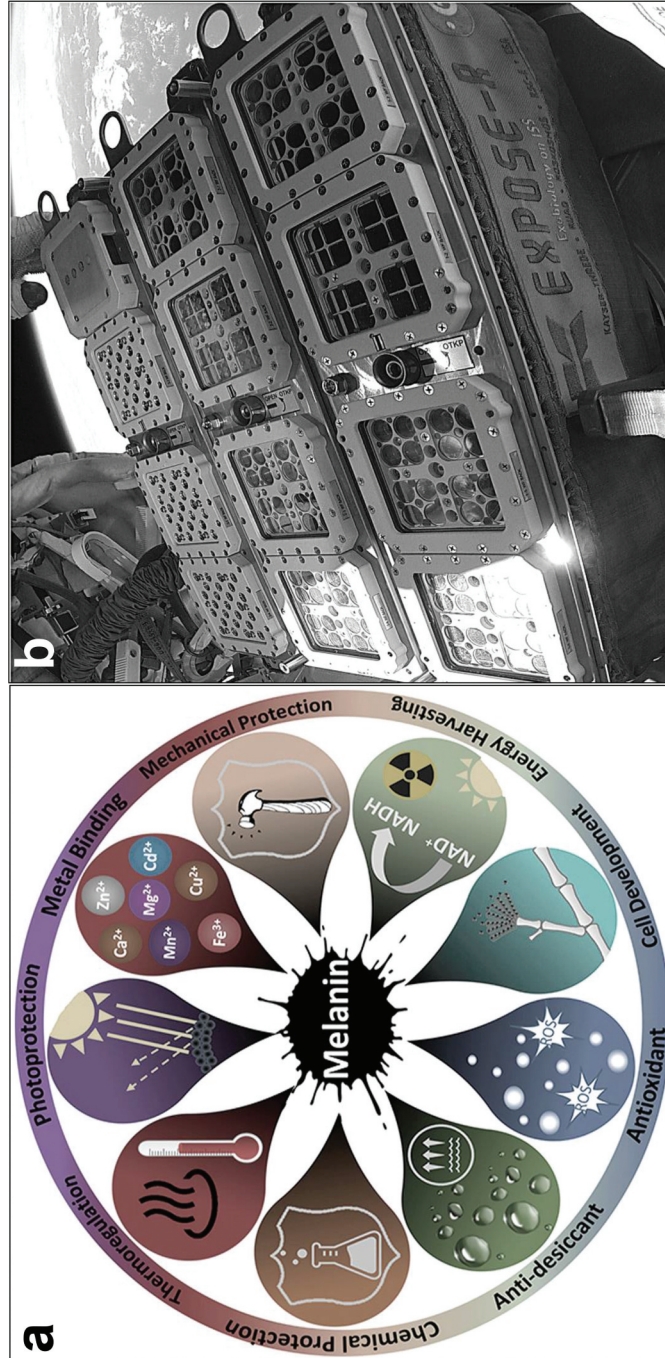


Figure 5. a. Functions of fungal melanins (Cordero and Casadevall 2017). Fungal melanins are critical for multiple biological functions, including photoprotection, energy harvest, and thermoregulation; they also function in free radical and metal binding and protection against dehydration and chemical and mechanical stressors. b. EXPOSE-R2 facility during exposure outside the International Space Station of the European Space Agency project BIOLOGY and Mars Experiment (BIOMEX) (Onofri et al. 2019).

communities (Selbmann et al. 2005, 2008); specifically, black yeasts belonging to Dothideomycetes, together with lichenized fungi, are predominant in these communities, whereas Eurotiomycetes are found less abundantly (Selbmann et al. 2017; Coleine et al. 2018a). In Antarctic endolithic ecosystems, black fungi are consumers of nutrients from the community and play a primary role in the protection of the whole community, forming a black “sunscreen” barrier just above the photobiont stratification (Selbmann et al. 2013). Several endemic taxa of black meristematic fungi, highly specialized to the extreme and with unique genotypes, have been described so far and continue to be found. A new species of the rock-inhabiting fungus *Lichenothelia antarctica* was identified from rocks in the Signy and Lynch islands, Antarctica (Øvstedal and Lewis Smith 2001).

The most extensive work on the diversity and taxonomy of black fungi from Antarctic rocks has been performed by Selbmann and collaborators. In over 20 years of Italian Antarctic campaigns, they have isolated and described numerous new taxa, mainly in the subclass *Dothideomycetidae*. Several species such as *Friedmanniomyces endolithicus* (FIG. 4d), *F. simplex*, *Cryomyces antarcticus* (FIG. 4e), *C. minteri*, *Rachicladosporium antarcticum*, *R. mcmurdoi*, *Extremus antarcticus*, *Meristemomyces frigidus*, *Vermiconia Antarctica*, and *Oleoguttula mirabilis* resulted as endemic, whereas others (e.g., *Recurvomyces mirabilis* and *Elasticomyces elasticus*) showed a worldwide distribution (Onofri et al. 1999; Selbmann et al. 2005, 2008, 2015; Egidi et al. 2014). Nearly all were characterized as psychrophiles and capable of growing from 0 up to 20 C, supporting the hypothesis that these organisms can survive in a highly variable environment characterized by dramatic thermal fluctuations, taking advantage of the thermal inertia of rocks, which can buffer changes and keep temperatures up to 20 C higher than the air (Selbmann et al. 2005, 2008).

In recent molecular-based surveys, targeting fungal internal transcribed spacer (ITS) region, Coleine and collaborators investigated the diversity and structure of the cryptoendolithic fungal community in sandstone samples collected along a gradient ranging from 1000 to 3300 m altitude. Authors found lichenized fungi prevailing in the northern sun-exposed surface, whereas black microcolonial fungi invariably predominated at the highest altitudes and southern expositions where conditions are much more extreme (Coleine et al. 2018a, 2018b, 2020d). More recently, an untargeted metabolomics revealed specific responses and adaptations to sun exposure. In fact, northern sun-exposed communities expressed a metabolite (allantoin) strictly related to the protection of photosystems from solar radiation, whereas southern communities on exposed

rocks expressed melanins, which protect against multiple stresses (Coleine et al. 2020a).

This finding is consistent with the peculiar ecology of these organisms that have high tolerance for low temperature and drought. In addition, these fungi are weak competitors, due to their poor metabolic competences and slow growth, and appear to be most successful where other microbes are constrained by environmental conditions.

In Antarctic endolithic communities, Dothideomycetes (e.g., *F. endolithicus*, *F. simplex*, and *E. antarcticus*) were found to be predominant. *C. antarcticus* was identified as a “core” member of these communities, suggesting that it may have a wider distribution in the continental Antarctica than previously hypothesized (Selbmann et al. 2012). Members of Herpotrichiellaceae (Eurotiomycetes), often associated with polluted environments, cold- and warm-blooded animals, were infrequently found (Selbmann et al. 2017; Coleine et al. 2018a). The highly specialized adaptation and the ecology of Antarctic RIF make them prone to climate change that may easily cause their extinction if milder conditions allow the settlement of more competitive species (Selbmann et al. 2012).

Unfortunately, research on environmental black fungi is hampered by their slow growth, resistance to genetic manipulation, and perhaps by the more specific focus on human-pathogenic species. Their extremely resistant cell wall with melanin encrustations and the presence of EPS make DNA extraction particularly challenging. Despite this, dozens of genomes from black fungi are now available, including several Antarctic cryptoendolithic specimens.

A few years ago, the first genome sequence of *Cryomyces antarcticus* (CCFEE 534) was published and compared with genomes of several species of black fungi isolated from diverse environments, resulting in a genome size of 24 Mbp. The preliminary analysis showed that “Nothing of special was found in the specialist,” as it showed a very small genome size (24 Mbp) and was found similar in size, content, and composition to the other black fungi considered (Sterflinger et al. 2014). After this pioneering study, a few reference genomes of Antarctic RIF were obtained. The genomes of *Rachicladosporium antarcticum* CCFEE 5527, *Rachicladosporium* sp. CCFEE 5018, *Exophiala mesophila* CCFEE 6314, *Horteaeta thailandica* CCFEE 6315, *C. antarcticus* CCFEE 534, *C. minteri* CCFEE 5187, *F. endolithicus* CCFEE 5311, and *F. simplex* CCFEE 5184 have been published recently (Sterflinger 2014; Coleine et al. 2017, 2019, 2020c). Most of these fungi have a higher DNA G+C content than other black fungi (Teixeira et al. 2017), and the genomes (35–50 Mbp) and proteomes (15 000–20 000 predicted protein-coding genes) are generally quite large. These observations support the

hypothesis that a whole-genome duplication occurred in Antarctic RIF and may have contributed to the important evolutionary processes that have enabled adaptation to highly specialized and extreme niches. To date, the halophilic black fungus *Hortaea werneckii* remains the only described example of a recent genome duplication or change in ploidy (Lenassi et al. 2013; Sinha et al. 2017; Gostinčar et al. 2018). Evidence of genomic changes that help organisms cope with low temperature, salt, X-rays, and DNA damage was found in *F. endolithicus* and confirms that this genus has exceptional polyextreme tolerance and the capacity to survive across a wide variety of stresses (Coleine et al. 2020c). One fungus, *F. endolithicus*, is the most widespread and abundant species in Antarctic cryptoendolithic communities, suggesting a high degree of adaptation to the prohibitive environmental conditions of the Antarctic desert. This species has been demonstrated to have resistance to acute doses of gamma radiation (up to 400 Gy) (Pacelli et al. 2018).

Further studies on black fungi are needed to elucidate the evolution, adaptation, and processes that govern their outstanding success in the extremes. With this in mind, the “Shedding light in the Dark Lineages of the Fungal Tree of Life” project (<http://www.stresblackfungi.org/>) aims to sequence up to 92 species of black fungal reference genomes, mostly from unsampled lineages, emphasizing a variety of ecologies and lifestyles, including rock-inhabiting fungi, for a comprehensive study of evolutionary processes and adaptations of these microorganisms across the extremes. In addition, metabolomics coupled with transcriptomics experiments on selected species across a range of stress conditions (salinity, dryness, UV radiation, oligotrophy) will reveal functions that may provide these microorganisms with evolutionary advantages.

Antarctic cryptoendolithic black fungi as test organisms for searching life beyond Earth. The adaptation over a timescale of evolutionary significance to the closest Mars-like conditions on Earth, and their ability to exploit the airspaces of rocks mimicking the endolithic colonization of a putative meteorite, makes Antarctic cryptoendolithic black fungi particularly suited as eukaryotic models for investigating the lithopanspermia theory and the possibility of extinct or extant life on the Red Planet (Onofri et al. 2004, 2008, 2012; Scalzi et al. 2012).

Within the framework of ESA and Italian Space Agency (ASI) programs, dehydrated colonies of the rock-inhabiting black fungus *C. antarcticus* (CCFEE 515) were exposed as part of the LIFE project for 18 months in the ESA EXPOSE-E facility to simulated Martian conditions aboard the International Space Station (ISS) (FIG. 5b). *C. antarcticus* CCFEE 515 has

been selected as the test organism also in additional astrobiological experiments, demonstrating its extraordinary ability to resist both ground-based and space experiments (Onofri et al. 2015, 2019; Pacelli et al. 2017), exhibiting also a stunning endurance after exposure to high doses of space-relevant gamma (^{60}Co ; up to 117.07 kGy), deuteron (^2H ; up to 1500 Gy), and sparsely ionizing (X-rays up to 300 Gy) radiation (Selbmann et al. 2018). It was also demonstrated that *C. antarcticus* not only survived extraterrestrial conditions in a dehydrated state but also remained in active growth, reacting to simulated Martian conditions by down-regulating protein expression, and recovered quickly its ability to grow when optimal conditions are restored (Zakharova et al. 2014). Additionally, in the framework of the BIOMEX project (FIG. 4e), conversely to the Antarctic endolithic lichen *B. frigida* (see above, Backhaus et al. 2019), the black fungus *C. antarcticus* was able to resist simulated space and Martian conditions (Onofri et al. 2019). The protective effect of melanin against UV and ionizing radiation has been well documented in black fungi (e.g., properties of melanin have been extensively discussed in Cordero et al. [2017] and Cordero and Casadevall [2020]). It is likely, therefore, that the highly melanized layer of *C. antarcticus* is the primary characteristic of its cellular phenotype and stress biology that may have enabled a superior performance during the 1.5-year exposure to extreme treatments compared with lichenized fungal species.

One of the main goals for astrobiologists is the definition of biosignatures (i.e., molecules indicating the presence of putative extinct or even extant life beyond Earth) (Horneck et al. 2016), representing a central focus and a challenge for the upcoming rover that is part of both the 2020 ExoMars mission (ESA/Roscosmos) and the Mars 2020 mission of the National Aeronautics and Space Administration (NASA). This previous work has contributed to melanin being counted as a potential biosignature (i.e., a molecule that indicate the presence of putative extinct or even extant life) that might occur in an extraterrestrial environment due to its high stability and broad distribution among all the kingdoms of life, suggesting an early emergence in the course of evolution. Melanins may also represent a valuable tool in the development of new protective materials; their capacity to absorb or screen multiple types of ionizing radiation and prevent the production of secondary radiation makes these biomolecules strong candidates for biomaterials for incorporation into irradiation protection in future manned space missions (Cordero 2017). Recently, the highly radiation-tolerant black fungus *C. antarcticus* was found to produce melanin via both 1,8-dihydroxynaphthalene (DHN) and L-3,4-dihydroxyphenylalanine (L-DOPA) pathways (Pacelli et al. 2020). These black yeasts

in extreme environments may be important for diverse melanin production

ANTARCTIC ENDOLITHIC YEASTS

Overview.—Yeasts reproduce asexually by budding or fission, producing single-cell stages, and have sexual structures not enclosed in a fruiting body (Kurtzman and Sugiyama 2015). This general definition includes both dimorphic lineages that produce mycelial growth in their sexual stages and biotrophic pathogens. Naranjo-Ortiz and Gabaldón (2020) recently proposed that the “yeast lifestyle” may be applied to unicellular or dimorphic fungi with a main unicellular stage in the environment and a highly limited extracellular metabolism. Yeast-like forms can be found in Ascomycota within the Saccharomycotina, the Taphrinomycotina, and in Basidiomycota within the Pucciniomycotina and the Ustilaginomycotina.

Yeasts, particularly from the Basidiomycota, are also common in frozen environments (Arendrup 2013; Turchetti et al. 2018) with limited water availability. The study of yeasts brings the potential for an industrially attractive low-temperature enzyme repertoire (Buzzini et al. 2012; Taskin et al. 2016; Martorell et al. 2017). Indeed, in addition to their ecology and role in fragile polar and mountain environments, the interest in yeasts inhabiting cold environments is due to the potential for biotechnological applications (Buzzini et al. 2012; Taskin et al. 2016; Baeza et al. 2017).

Ecology and taxonomy of Antarctic endolithic yeasts.—Yeasts constitute an important part of psychrophilic microbiomes in Antarctic ecosystems, including the endolithic microbial communities, representing metabolically active organisms (Friedmann 1982; Selbmann et al. 2014d). Barahona et al. (2016) reported that yeasts isolated from Antarctic rocks produced various carotenoid pigments or mycosporines, suggesting an evolutionary response to oxidative stress induced by UV radiation and other factors prevalent in this region. Vishniac and Hempfling (1979a, 1979b) isolated some yeasts from Antarctic rocks, and a few years later Vishniac (1985) described the species *Naganishia friedmannii* (initially described as *Cryptococcus friedmannii*) that appeared rather physiologically dissimilar from all other known basidiomycetous yeasts. This species has been proposed to be a secondary consumer in the endolithic community, utilizing traces of available substrates released by lysis of other community microbiota.

A few years ago, in a worldwide rocks survey, Selbmann and colleagues (2014d) confirmed the endemic nature of

Cryptococcus vishniacii, which has been isolated exclusively from Antarctic rocks, whereas *N. friedmannii* has a worldwide distribution and has been isolated in other cold habitats such as Arctic permafrost (Faizutdinova et al. 2005) and Alpine glaciers (Turchetti et al. 2013). Almost all isolates were psychrotolerant and belonged mainly to Basidiomycota, whereas about 40% of yeast isolates belonged to undescribed species; *Cryptococcus* (including some anamorphic states of teleomorphic genera of orders Filobasidiales and Tremellales) and *Rhodotorula* (order Cystobasidiales) were the most frequent genera both in Antarctic rock and soil communities (Connell et al. 2014; Coleine et al. 2020b). Selbmann et al. (2014c) also related the ability of yeasts to assimilate different carbon and nitrogen sources to their ecology: they found that species with an apparent global distribution exhibited a wider assimilation pattern and may be considered to be facultative oligotrophs; conversely, species with a more restricted distribution, or even endemic to the Antarctic, showed a narrower metabolic profile, suggesting a rather oligotrophic tendency.

With the development of culture-independent molecular methods, such as environmental DNA, a more accurate census of the yeasts in these microbial consortia has been possible. Coleine et al. (2018a, 2018b, 2020d) found that Basidiomycota represent recurring community members, identified as *Cryptococcus* sp. Members of Saccharomycetes (Ascomycota), never isolated so far from Antarctic cryptoendolithic communities, have been retrieved, even at the lowest frequency, suggesting that basidiomycetous yeasts may be more adapted to selective pressures of cold regions compared with ascomycetous ones (Vishniac 2006; Connell et al. 2008). The presence of a thicker cell wall and the ability to produce an EPS capsule may have given a selective advantage in hostile environments to basidiomycetous yeasts. However, due to their relative abundance and saprotrophic ecology in different niches, authors have supported the idea that yeasts may play an important role as degraders in these communities.

Yet, the physiological opportunistic virulence potential of an endolithic yeast, *Rhodotorula mucilaginosa*, has been evaluated in vitro; authors found that this strain was able to grow at 37 C and suggested that rocks of the extremely cold and dry environment of Antarctica may harbor cryptic fungi phylogenetically close to opportunistic pathogens (Gonçalves et al. 2017).

New comparative techniques such as high-throughput sequencing will offer the opportunity to further explore the potential pathogenicity of Antarctic endolithic yeasts and how they evolved and adapted at the edges of life.

Adaptation of *Taphrina antarctica* to Antarctic desert conditions. One of the most notable examples of novel yeast species from Antarctic rocks is undoubtedly *Taphrina antarctica* (FIG. 4f), described by Selbmann et al. (2014c). *Taphrina* spp. show a dimorphic lifestyle; whereas the teleomorphic filamentous state lives exclusively as biotrophic plant pathogen on Rosaceae, Betulaceae, and Fagaceae, the anamorphic states are capable of saprobic growth. This was the first report of strains belonging to the genus *Taphrina* from substrates other than a plant, especially in the Antarctic desert. This finding was particularly surprising because the continent is devoid of plants and only two phanerogams have been described on the Antarctic Peninsula. The authors have suggested that this species may have adapted to life on rocks by permanently switching to a yeast-like asexual saprotrophic lifestyle. This ability may have provided advantage by saving life costs and enabling this species to explore new extreme ecological niches such as microbial rock-inhabiting communities. Yet, it has been hypothesized that even if this species has preserved the ability to parasitize its natural host, it is now extinct in the Antarctic continent and, possibly, in other regions. Ecologically speaking, the inability of *T. antarctica* to grow above 20 C makes this species an obligate psychrophile, and it may develop a set of adaptive strategies to overcome the negative effect of cold, producing cold-shock and antifreeze proteins.

Further investigations, using a wider number of Antarctic endolithic isolates, are needed to elucidate the evolution, diversity, and distribution; future omics approaches may provide tools for understanding the ecological role of the genus *Taphrina* in the Antarctic cryptoendolithic communities.

MARITIME ANTARCTIC FUNGAL ROCK COMMUNITIES

Terrestrial ecosystems in Antarctica are restricted to a few permanently ice-free areas (less than 1% of the continent) (Lee et al. 2017), spanning from the deserts, nunataks, and mountains of the inner regions to the moist cryptogam-dominated coastal areas (Fretwell et al. 2011). Rogers (2007) classified terrestrial Antarctica into three zones according to geographic, climatic, and biotic characteristics: the sub-Antarctic, the maritime Antarctica (that includes the South Shetland Islands and the western side of the Antarctic Peninsula), and the continental Antarctica. Most of the available knowledge from Antarctic lithobionts comes from rocks collected on continental Antarctica, mainly from the Ross Desert (Makhalanyane et al. 2014). Here, higher plants and animals are absent and epilithic colonization by lichens is scarce (de los Ríos et al. 2014;

Goordial et al. 2017). Conversely, maritime Antarctic climatic conditions are less extreme than those of continental Antarctica, and different forms of living organisms are present (including penguins, seals, sea lions, and birds during the summer season). Mosses, liverworts, and lichens are common in the ice-free zones, and even two angiosperms, *Deschampsia antarctica* and *Colobanthus quitensis*, are present.

Alves and colleagues (2019) aimed to characterize the richness, diversity, distribution, and ecology of fungal communities present in rocks from various Antarctic islands, as well as to evaluate their virulence potential to humans through in vitro assays. Fifty rocks were collected from King George, Penguin, Nelson, Robert, Half Moon, Livingston, and Deception islands in the 2013 austral summer. Almost 400 fungal isolates were obtained, among which the cosmopolitan *Paracladophialophora* and *Penicillium* displayed the highest frequency. Other fungi with polar distribution such as *Auricularia*, *Cyphellophora*, *Cladophialophora* (a black yeast-like human pathogen), and *Thelebolus* were also detected. Members of *Cyphellophora*, *Fusarium*, and *Cladosporium*, typically observed in association with plants as endophytes or phytopathogens, were also isolates from rocks collected in proximity of the two mentioned plants *D. antarctica* and *C. quitensis*. Ecological diversity indices showed that the fungal assemblages were more diverse and richer than those present in other Antarctic endolithic habitats from Victoria Land (continental Antarctica) (see Coleine et al. 2018a, 2020d). Additionally, more than a hundred species isolated, including *Penicillium chrysogenum*, *Fusarium* sp., and *Rhodotorula mucilaginosa*, were able to grow at 37 C and displayed hemolytic activity and dimorphism. According to these findings, the authors hypothesized that these microbial communities may be a vehicle for the dispersal of fungal propagules, including across and out of the continent.

Garrido-Benavent and collaborators (2020) have recently analyzed the dynamics of fungal colonization at moraine rocks from a chronosequence of a maritime Antarctic glacier forefield. Distinct succession patterns were detected for different fungal taxonomic groups: whereas *Eurotiomycetes* and *Lecanoromycetes* increased in abundance with time, being ice-free, *Tremellomycetes* and *Ustilagiomycetes* decreased. Endolithic lichens were not detected at initial succession stages, but they occurred in parallel with the establishment of epilithic lichen thalli at the latest analyzed succession stage.

ROCKS AS A WORLDWIDE REFUGE FOR FUNGI

The endolithic habitat is ubiquitous in hot, cold, and polar deserts around the world, and endolithobionts

play key roles in the functioning and balance of these ultimate ecosystems in extreme environments. However, a comprehensive knowledge of rock-inhabiting fungi and their ecological preferences at the global scale is still lacking, and the current knowledge will be summarized in this section.

Atacama Desert and other hot, arid regions.—Beyond Antarctica, the Atacama Desert in northern Chile is well studied for its endolithic ecosystems (FIG. 6a, b). The Atacama Desert is an exceptional polyextreme environment that is considered the driest and most life-limited place on Earth, with the lowest annual rainfall and highest UV and solar irradiance ever measured. These deserts and their rocks have been considered devoid of life for many years. The terrestrial extremes are considered a Mars analogue, and the Atacama Desert is used for testing of the instrumentation on future payloads of Martian missions (Vítek and Wierzchos 2020).

The hyperarid core, extending across 1000 km from 30°S to 20°S up to 3500 m a.s.l., is counted as one of the closest analogues of the extreme arid conditions on the Red Planet, and an ideal environment to explore survival and biological adaptation strategies of life. The first evidence of an endolithic microbial community in the hyperarid core of the Atacama Desert was observed within the halite (NaCl) rocks of the Yungay area (Wierzchos et al. 2006). Most of the subsequent studies in this region focused on prokaryotes (e.g., see de los Ríos et al. 2010; Stivaletta et al. 2012; DiRuggiero et al. 2013; Vítek et al. 2013; Davila et al. 2015; Robinson et al. 2015; Crits-Christoph et al. 2016; Meslier et al. 2018; Wierzchos et al. 2018), whereas our overall knowledge on fungi remains largely limited (Wierzchos et al. 2011), hampering our understanding of their potential role within this hyperarid region. Further research is thus clearly necessary to explore the diversity, ecological roles, and biotechnological potential of fungi living inside these rocks.

Gonçalves and collaborators reported a new habitat of fungi associated with rocks collected from a range of elevations of the Atacama Desert and noted a highly diverse fungal community, including species similar to known saprobes, parasites/pathogens, and mycotoxigenic taxa (Gonçalves et al. 2016). The authors isolated 81 fungal strains from rocks incubated at 25 C for 60 days; most of them were identified as Ascomycota species of the classes Dothideomycetes, Sordariomycetes, Eurotiomycetes, and Leotiomycetes. The most predominant genera were *Alternaria*, *Aspergillus*, *Cladosporium*, *Cochliobolus*, *Devriesia*, *Eupenicillium*, *Fusarium*, *Pseudogymnoascus*, *Hypoxylon*, *Macroventuria*, *Neosartorya*, and *Penicillium*.

This list of genera does not include rock specialists; the taxa belonging to *Alternaria*, *Cladosporium*, and *Penicillium* are wind-dispersed generalist Ascomycota genera and well known to occupy multiple environmental niches, and they have been also found within the <0.1% of globally dominant soil fungi (Egidi et al. 2019).

Several taxa isolated from this survey are sources of bioactive metabolites; most of them are considered important prototype molecules used in the development of new drugs to find new bioactive constituents. Specifically, the isolate *P. chrysogenum* UFMGCB 8074 was shown to produce the compounds α -linoleic acid and ergosterol endoperoxide, which were identified as active against fungal and bacterial targets (Gonçalves et al. 2016). The carboxylic acid, α -linoleic acid, is known to have antibacterial, antimycobacterial, and antifungal activities (Pohl et al. 2011).

More recently, the first shotgun metagenomic-based analysis on halite endolithic communities from Salar Grande in the Atacama Desert has been reported (Gómez-Silva 2018; Gómez-Silva et al. 2019). The authors analyzed microbial diversity (including archaea, bacteria, and fungi), indicating that the microbiome is typically composed of NaCl-adapted microorganisms, and reported a limited diversity of fungal families, with the Aspergillaceae, Sporidiobolaceae, and Sordariaceae being the most highly represented. *Rhodotorula*, *Sordaria*, and *Aspergillus* were the most prevalent contigs classified at the genus level. The recurrent isolation of *Rhodotorula* species from several hypersaline environments clearly demonstrates that this genus is highly ubiquitous and is distributed worldwide. The abundance of *Aspergillus* agrees with a culture-based taxonomic study from other sites in the Atacama Desert (Yungay halites) (Culka et al. 2017).

North American drylands and Chinese deserts also represent a reservoir of endolithic fungi. First reports of microcolonial rock fungi from the Mojave Desert and Arizona were published by Nash and colleagues (1977) and, a few years later, by Staley et al. (1982), respectively. Members of *Lichenothelia* (Dothideomycetes, Ascomycota), which has been hypothesized to represent a link between rock-inhabiting meristematic fungi and lichenized fungi (Muggia et al. 2013), were isolated from the Sonoran and Mojave deserts and Joshua Tree National Park in California (Muggia et al. 2015).

Endolithic lichenized fungi have been observed in other hot deserts such as the Namib Desert (FIG. 6c, d). Tang and colleagues were among the first to study endolithic communities from Nanjiang Canyon in Guizhou area (a typical karst canyon in China), studying dolomite and limestone escarpments present beneath an overlying layer of vegetation and accumulated organic matter. *Aspergillus* spp. and *Penicillium* spp. were the most frequently recorded, whereas other strains were identified as

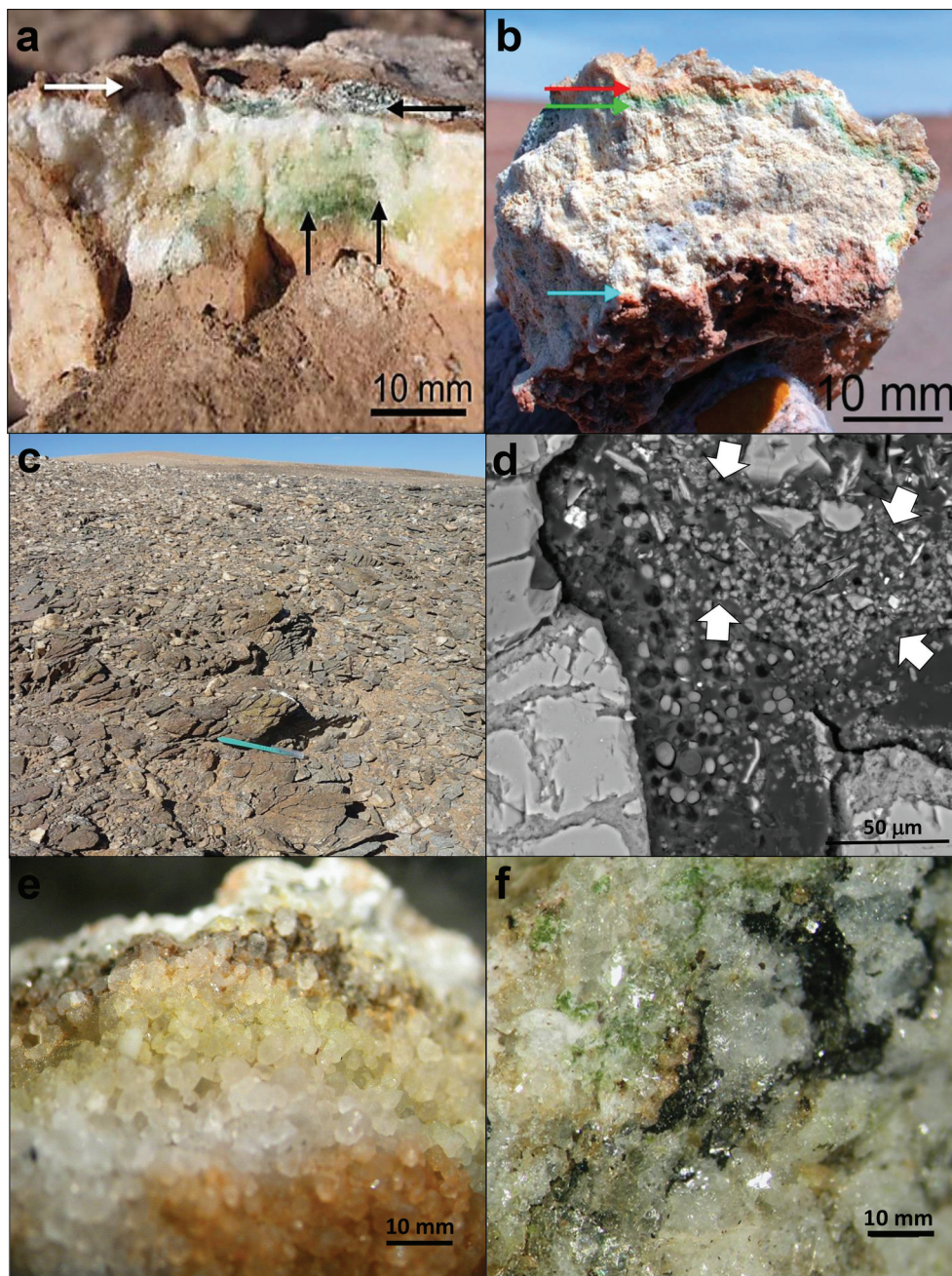


Figure 6. Examples of endolithic communities from worldwide drylands. a. Endoliths (black arrows) colonizing calcite fissures in the Atacama Desert (northern Chile); white arrow indicates the presence of a hardened surface layer (DiRuggiero et al. 2013). b. Cross-section of gypsum cryptoendolithic (red and green arrows) and hypoendolithic (blue arrow) microbial colonization from Atacama Desert (Wierzchos et al. 2015). c. Sampling in Namib Desert in the proximity of Gobabeb Desert Research Station (Namibia). d. SEM-BSE image of lichen association occupying a fissure of granites from Namib Desert. Arrows indicate accumulation of calcium oxalate. e–f. Cryptoendolithic communities from Stolemberg (3200 m a.s.l.), Mt. Rosa, Italian Alps.

Aureobasidium pullulans, *Paecilomyces*, *Alternaria*, and *Fusarium*. Using the restriction fragment length polymorphism (RFLP) molecular approach, lichen-forming fungi (i.e., *Verrucaria* and *Caloplaca* spp.) were also obtained (Tang and Lian 2012; Tang et al. 2016). In these works, due to the high relative abundances, *Aspergillus* and *Penicillium* have been proposed to

commonly occur in these endolithic ecosystems. Since these genera do not include rock specialists, their presence is most likely related to the reported high organic matter content in the rock samples resulting from associated vegetation.

Despite that members of *Aspergillus* spp. have been associated with oligotrophic soils (Godinho et al. 2015;

Figueredo et al. 2020) as well as Atacama and Antarctic rocks (see Gonçalves et al. 2016; Culka et al. 2017; Coleine et al. 2018a; Gómez-Silva et al. 2019), we propose that the occurrence of these filamentous fungi in the desert data set is more likely the result of a postsampling contamination, rather than the reflection of a true component of the endolithic mycobiome.

Indeed, the environmental pressure typically associated with the exposed bare rocks requires a high degree of adaptation and specialization, suggesting that this substratum may be not suitable for fast-growing, cosmopolitan taxa, such as members of the above-mentioned genera. Furthermore, Tang et al. incubated fungi for 7 days only, and in view of numerous slow-growing fungi colonizing rocks, this time could be inadequate; with longer periods of time (up to several months), it is possible that a more realistic and abundant fungal diversity would have been retrieved. Moreover, successful isolation procedures to obtain rock fungal specialists must imply a thorough washing of rock samples to remove contaminants as much as possible and the use of poisoned media such as dichloran rose Bengal agar (DRBC) to retard the growth of the residual cosmopolitan and fast-growing microbes. Thus, it is evident that additional detailed studies of endolithic fungi need to be attempted to elucidate the actual role of filamentous fungi within the rocky niches.

High-altitude regions.— Although much early work on endolithic communities has stressed their prevalence in extremely hot and cold deserts, geographically microbial colonization in rocks has been observed in a variety of extreme terrestrial ecosystems, including even the geothermal environments. The discovery of endolithic communities inhabiting the pore space of rocks in (pH 1) of Yellowstone National Park (USA) was of paramount importance. Walker and collaborators isolated total DNA from rock samples and used universal polymerase chain reaction (PCR) primers targeting all three domains; they found Chlorophyta, Actinobacteria, and Cyanobacteria to be predominant members, whereas no evidence of fungi was observed (Walker et al. 2005). We here propose that further culture-based and amplicon experiments should be performed on these extreme environments to further test for absence of black yeasts, which have demonstrated a propensity for adaptation to these conditions. For instance, fungi within the genera *Acidomyces* and *Hortaea acidophila* are able to grow at pH 1, with an optimal growth rate at below the neutral pH value (pH 3–5) (Hölker et al. 2004; Selbmann et al. 2008).

Fungi inhabiting terrestrial endolithic habitats are also widespread in high-altitude regions (Wong et al. 2010;

Muggia et al. 2015; Ametrano et al. 2017) and temperate climates even in the Canadian high Arctic (Omelon et al. 2007; Rhind et al. 2014). For example, 28S rRNA amplicon sequences assigned to Dothideomycetes (orders Capnodiales, Dothideales, Myriangiales, and Botryosphaeriales) and Eurotiomycetes (order Chaetothyriales) predominated in fungal endolithic communities from Svalbard (Norwegian high Arctic), with the observation of members of the Leotiomycetes and Sordariomycetes (Choe et al. 2018). The latter contain species known as producers of some of the most important fungal secondary metabolites that may play an important role in having strong UV absorption abilities.

Selbmann and coworkers focused their efforts on black fungi, contributing to the knowledge on their ecology and dispersal mechanisms. As part of a worldwide sampling, they described several new fungal genera (e.g., *Monticola*, *Catenulomyces*, *Incertomyces*, *Petrophila*, and *Vermiconia*) and species (e.g., *Cryomyces montanus*), mainly in Dothideomycetes, from rocks collected from Mount Aconcagua (Andes), the Mediterranean (Sardinia, Mallorca), Indian Himalayan, and Italian Alps (FIG. 6e, f) (Selbmann et al. 2008, 2014b; Egidi et al. 2014).

The species *Recurvomyces mirabilis* and *Elasticomyces elasticus* are found in cold, dry environments but display a worldwide distribution, suggesting that even nonsporulating rock-inhabiting fungi may occasionally be dispersed between continents (e.g., via dust) and adapt to other ecologically similar, but geographically remote habitats, beyond Antarctica. Two new *Cryomyces* species, phylogenetically very distantly related to the Antarctic species *C. minteri* and *C. antarcticus*, were isolated from the Alps; *C. montanus* CCFEE 5554 was even able to grow at 30 C; this thermal profile is rather frequent in microorganisms from cold areas characterized by highly fluctuating temperatures as adaptation to thermally unstable environments.

Although isolation of yeasts from extreme habitats is difficult because many of them could not be cultured under laboratory conditions (Boundy-Mills 2013) and an accurate estimate of yeasts diversity in worldwide rocky habitats is nowadays not possible, a few works reported evidence of endolithic yeasts from cold regions (Selbmann et al. 2014c; Turchetti et al. 2018). In agreement with the yeast diversity found in over 60 years of studies on microbial communities of cold ecosystems, recently reviewed by Buzzini et al. (2012, 2018), the basidiomycetous *Cryptococcus* (orders Filobasidiales and Tremellales) and *Rhodotorula* (order Cystobasidiales) were the most frequent genera, confirming the ability of basidiomycetous yeasts to colonize unusual niches. In contrast, the species *Taphrina antarctica* has only been described and recorded in endolithic Antarctic communities (Selbmann et al. 2014a).

Endolithic fungal “core” community.—Several years ago, Walker and Pace (2007) formulated the “metacomunity” concept, hypothesizing that endolithic ecosystems are seeded from a relatively limited reservoir of phylogenetic diversity uniquely adapted to the endolithic niche. They compared endolithic communities from a few extreme environments, namely, Rocky Mountains (Canada), Yellowstone National Park (California, USA), and McMurdo Dry Valleys (continental Antarctica); they found that all communities shared several bacterial and algal sequences (mostly at phylum taxonomy level) that are 98% identical, whereas fungal phylotypes (33) have been solely observed in Antarctic samples. Although we understand the value of their proposal, we advise caution regarding the robustness of this hypothesis; at least, general considerations may not be extended to genera and species levels. The “metacomunity” concept is, nowadays, not applicable to fungal endoliths, as an adequate understanding of fungal endolithic diversity is limited to Antarctic fungal assemblages but their community makeup globally remains unevenly explored. Several efforts reported that most major lineages of endolithic fungi belong to Dothideomycetes and Eurotiomyces (Ascomycota) (lichen-forming fungi and black fungi) and yeasts (in particular *Rhodotorula* and *Cryptococcus*) are placed mostly in Basidiomycota. Many of the isolated strains are endemic and have frequently represented undescribed species, confirming the endolithic communities as a reservoir of new extreme-tolerant and extremophilic fungi. A few black yeast genera such as *Devriesia*, *Cryomyces*, *Recurvomyces*, and *Elasticomyces* are found in multiple geographic locations, showing a global success. Due to the lack of an accurate record of endolithic fungi across the globe, the evidence supporting the “metacomunity” hypothesis is only circumstantial. Indeed, shifts in fungal community composition have been reported in different rock typologies, even in sandstone samples collected in the same locality (Coleine et al. 2020e), whereas a few fungi occur as ‘core’ members (species shared across different endolithic ecosystems) (Coleine et al. 2018a, 2020d). Besides, the advances of high-throughput sequencing now allow detecting many cryptic rare taxa, whereas Walker and Pace’s (2007) work is based on standard, low-taxonomic-resolution methods. Thus, based on our synthesis, we may redefine the “metacomunity” concept and herein propose the new concept of “endolithic fungal ‘core’ community,” laying the foundation to the hypothesis that a widespread occurrence and abundance of a few fungal species can occur in rocks of arid and hyperarid areas, sharing traits that allow them to adapt up to the dry limit for life. Besides,

additional studies are needed to better clarify the occurrence and distribution of rock-inhabiting fungi in desert regions and test whether all these fungi share adaptation strategies to environmental constraints (e.g., evolving similar growth and reproductive/dispersal strategies to colonize endolithic microhabitats). Determining which fungi are dominant in dryland rocks, and the environmental variables that drive their abundance and distribution, will constitute a major scientific advance.

CONCLUDING REMARKS

Although extreme conditions on drylands limit life, fungi often inhabit the interior of different rock typologies in these areas, either by symbiotic associations or as a free-living form. In these extreme ecosystems, the endolithic communities contribute to the weathering of the rocks, playing a potential key role in soil formation, and are generally composed of both endemic taxa with very peculiar physiological traits and cosmopolitan species. The apparent simplicity of lithobiontic communities makes them among the simplest microbial ecosystems known and thus model systems for exploring trophic functioning and interspecies relationships and for addressing even wider macroecological questions. Despite that, a systematic and comprehensive assessment of the diversity and taxonomy of endolithic fungi across the globe is still lacking. Indeed, studies hitherto conducted on worldwide endolithic communities supplied only patchy information on their biodiversity, since analyses are limited to a few rocks or from on single desert, whereas comparisons among drylands, geographic locations, and different climatic conditions are still missing.

A more extensive survey at the global scale of endolithic communities is necessary in order to obtain a deeper and comprehensive view of occurrence, distribution, and adaptation of rock-inhabiting fungi. Determining which fungi are dominant in dryland rocks, and the environmental variables that drive their abundance and distribution, will constitute a major scientific advance.

Although with several methodological limitations (biomass levels and intrinsic process rates are typically low in endolithic communities), high-throughput sequencing, in the last two decades, has significantly contributed to characterizing the richness and distribution of fungal endolithic communities than culture-based methods, but the approach yields limited information about the physiology or ecology of community members. We, therefore, recommend that a combination of both culturomics and whole-community molecular approaches should be used to provide a more accurate description of endolithic fungal communities. We also propose that protocols need to be optimized for these endolithic environmental samples

and consistently applied by researchers from all over the world (e.g., using amplicon sequencing approach targeting both fungal ITS1 and ITS2 regions). Isolation itself should be as selective as possible; for instance, for meristematic fungi, growth-inhibiting media should be used to limit growth of contaminants such as cosmopolitan airborne fungi that, to some extent, are found in the endolithic communities but may not be actually members of these microbial ecosystems. A multiphasic approach combining culturomics and high-throughput, culture-independent methods will characterize the fungal communities inhabiting these rock habitats and identify potential factors driving their colonization.

A global rock survey may be helpful to (i) understand the composition, functionality, and resilience of endolithic fungi; (ii) develop tools to inform potential effects of environmental change to endangered desert landscapes; and (iii) apply strategies to management and preservation of worldwide drylands, in an era of rapid desertification.

ACKNOWLEDGMENTS

Don Cowan (University of Pretoria) and Gillian Maggs-Koelling and Eugene Marais (Gobabeb Research and Training Centre) are thanked for facilitating the collection of Namib samples for microscopy studies and Allan Green and Chris P. McKay for the Antarctic ones.

FUNDING

C.C. and L.S. wish to thank the Italian National Program for Antarctic Research for funding sampling campaigns and research activities in Italy in the framework of Italian National Program for Antarctic Researches (PNRA) projects. The Italian Antarctic National Museum (MNA) is acknowledged for financial support to the Mycological Section of the MNA and for providing rock samples used in the investigations and stored in the Culture Collection of Fungi from Extreme Environments (MNA-FCC), University of Tuscia, Italy. J.E.S. is a CIFAR fellow in the Fungal Kingdom: Threats and Opportunities program. A.d.l.R. acknowledges financial support of the grant CTM2015-64728-C2-2-R (MINECO/FEDER, UE) for microscopy analysis.

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