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Ecophysiology and biotechnological potential of rock-inhabiting fungi in mineral substrate degradation and conservation

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Abstract

Rock-inhabiting fungi are a remarkable group of microorganisms that thrive on mineral substrates and exhibit exceptional resilience and adaptability in extreme environments. This review discusses the role of rock-inhabiting fungi in bioweathering in terms of their physiology, ecology, adaptations, and impact on environmental processes. It also discusses the fungal diversity and the taxonomy of fungi found on rocks and cultural monuments. it also emphasizes their ecological importance and implications on the conservation of heritage sites.

Bioweathering by fungi involves intricate mechanisms such as organic acid secretion, enzymatic activity, and mechanical processes, which facilitate mineral decomposition and nutrient cycling. Advanced methods, including molecular techniques, microscopy, and biochemical analyses, are instrumental in unraveling the diversity and functionality of these fungi. The review also explores innovative research approaches and the environmental implications of rock-inhabiting fungi, emphasizing their role in sustainable applications, including the restoration of cultural heritage and ecological remediation.By synthesizing current knowledge and addressing gaps in understanding, this paper underscores the need for interdisciplinary research to fully exploit the potential of rock-inhabiting fungi in biotechnology and environmental conservation. The findings contribute to a deeper understanding of fungal bioweathering processes and their relevance to both natural and anthropogenic ecosystems.

Key words: Bioweathering, Ecophysiology, Fungi, Heritage, Rock-Inhabiting fungi

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Introduction

Rocks represent one of the oldest and most widespread terrestrial habitats for life on Earth. Throughout the evolutionary history of fungi, certain species have adapted to inhabit rocks, forming black microcolonies on rock surfaces. These fungi are typically slow-growing, produce melanin, and primarily develop through meristematic or yeast-like forms. These characteristics have led to various terminologies such as microcolonial fungi, meristematic fungi, or black yeasts, depending on their morphological or physiological perspectives (Sterflinger, 2006). In contrast to lichens, symbiotic assemblages of a fungal mycobiont and a photosynthetic partner (green algae or cyanobacteria), rock-inhabiting fungi (RIF) are non-lichenized, free-living heterotrophic eukaryotes that lack photobionts, forming slow-growing, melanized colonies that are far less conspicuous than lichen thalli. These fungi can thrive in a range of extreme environments, from tropical deserts to humid Mediterranean coasts and the McMurdo Dry Valleys in the Antarctica, enduring stresses like solar radiation, desiccation, rehydration, and temperature fluctuations (Onofri *et al.,* 2014).

The initial meticulous academic studies of rock-inhabiting fungi began with the work of Staley *et al.* (1982), who observed dark microcolonial structures on bare rock surfaces using scanning electron microscopy (SEM) and detected high rates of physiological activity through respiration measurements. This work was further substantiated by isolating pure cultures of black fungi capable of recolonizing sterile marble in laboratory conditions. Microscopic observations have revealed limited diagnostic features based on their meristematic or yeast-like development and a lack of typical sporification structures (Gorbushina *et al.,* 2009). Molecular phylogenetic analysis has been pivotal in reliable species delimitation of rock-inhabiting fungi. Many microcolonial black fungi have been identified as new species and higher taxonomic ranks in recent years (Isola *et al.,* 2022; Sun *et al.,* 2020). These fungi are affiliated with classes such as Dothideomycetes, Eurotiomycetes, and Arthoniomycetes within the Ascomycota (Gueidan *et al.,* 2011; Ruibal *et al.,* 2009). Phylogenetic frameworks for rock-inhabiting fungi within Dothideomycetes have been proposed at the order or family level (Ruibal *et al.,* 2009; 2011).

Terminology and classification: Rock-inhabiting fungi broadly emphasize the habitat of fungi on rocks. It excludes transient colonizers and dormant spore contaminants without physiological activity (Sterflinger *et al.,* 2012). These fungi colonize various rock types like Lameta rock formations, which have various layers (Fig. 1). Lithobiontic fungi are derived from Greek. This term refers to fungi living on or inside rocks, encompassing slow-growing black yeasts or molds. Specific terms like epilithic, chasmolithic, and endolithic describe fungi colonizing rock surfaces, fissures, and interiors, respectively (Miura and Urabe, 2017). The term microcolonial fungi (MCF) was proposed by Staley *et al.* (1982). This term refers to fungi forming microcolonial structures on mineral substrates. These fungi exhibit meristematic or yeast-like growth. The term meristematic fungi describe fungi that reproduce by isodiametric division, forming aggregates of melanized cells. Black yeast refers to fungi with melanized cell walls that reproduce by yeast-like budding. Black yeasts may also exhibit mycelial growth and conidia formation (Sterflinger, 2006). The Melanized/ Black/ Dematiaceous Fungi term is used to describe fungi that produce black pigments like melanin. "Melanized" is more accurate and frequently used, especially in contrast to "non-melanized" mutants (Dadachova *et al.,* 2007). Lithophilic/ Lithotolerant Fungi describe fungi living in rocky habitats, either benefiting from the rock niche (lithophilic) or tolerating pressure of rock environments (lithotolerant). Lithophilic fungi grow extremely slowly, while lithotolerant fungi grow relatively faster (Fig. 2).

Fig. 1: Lameta rock formations, highlighting distinct geological zones that categorize the formations based on lithological characteristics, composition, and environmental influences.

Physiology and adaptation mechanisms: Rock surfaces are nearly nutrient-free. Therefore, the physiology of rock-inhabiting fungi is more of an oligotrophic nature, conserving energy and enhanced stress-tolerance (Coleine and Selbmann, 2021). These fungi can survive without organic carbon, nitrogen, and with minimal moisture. One of the main strategies is the profound metabolic downregulation wherein many unicellular fungi survive in dormant, meristematic, or yeast-like microcolonial cells embedded in extracellular polymeric substances (EPS). They resume the radial or budding growth only upon episodic hydration and under strictly limited caloric budgets. In this process, they express only a small core set of proteins and conserve energy (Zakharova *et al.,* 2014a, b; Liu *et al.,* 2022). Morphological elasticity, interchanging between spherical meristematic forms,

Fig. 2: Key terminologies related to rock-inhabiting fungi.

which reduces the surface to volume ratio and hyphal form, and can penetrate using hyphal pegs into rock crevices. This increases the protection from UV radiation, harsh temperatures, and other environmental fluctuations while surviving on minimal nutrition in micro niches (Connell *et al.,* 2009).

Fungi can survive in an oligotrophic environment due to melanin, as it provides mechanical stiffness, resists acid hydrolysis, heavy metal toxicity, and provides effective protection from radiation such as UV and Gamma rays. This is achieved with the help of multilayered melanized coats composed of dihydroxynaphthalene melanin attached to chitin and β-glucan. Melanin also reduces desiccation through retention of hygroscopic water and antioxidant activity, buffering reactive oxygen species, and altering cellular permeability in these rock-inhabiting fungi (Garcia-Rubio *et al.,* 2020). In fungi, melanosomes contain melanin interposed between EPS layers and polysaccharide scaffold, forming a tough protective matrix (Camacho *et al.,* 2019). These fungi also synthesize small protective osmolytes and pigments such as trehalose, mannitol, glycerol, carotenoids, and mycosporines. These play an important role as osmoprotectants, UV filters, antioxidants, and enzyme stabilizers during desiccation or thermal stress. In dehydrated cells, trehalose and mannitol concentrations exceed 40% of total cytosolic carbohydrates under low-water or high-temperature conditions. This prevents protein denaturation and preserves membrane integrity (Liu *et al.,* 2022). Most of the rock-inhabiting fungi have to face acidic microhabitats consisting of silica or mineral surfaces. Rain or biofilm metabolism lowers pH, maintaining an intracellular pH homeostasis via conserved fungal pH signaling pathways. The proteolytic activation cascade (PacC) in fungi senses external acidity. It triggers transcriptional reprogramming of cell wall remodeling, proton pump expression, and secretion of protective extracellular compounds under acid stress (Lara-Martínez *et al.,* 2025; Ramírez-Sotelo *et al.,* 2025). Acidophilic fungi like *Phlebiopsis gigantea* accumulate trehalose and polyols at low pH, and proton pumps, along with phospholipid composition, help maintain membrane stability (Ianutsevich *et al.,* 2023). Environmental signals such as osmotic or desiccation stress trigger high osmolarity glycerol (HOG) and cell wall integrity (CWI) MAPK pathways. These pathways rapidly induce heat shock proteins, upregulate solute synthesis, and enhance chitin deposition, stiffening the wall against shrinkage or water loss. In sun-scorched rock, overlapping stress pathways further adjust metabolism through transcription factors to a unified environmental stress response (Ianutsevich *et al.,* 2024). The physiology of rock-inhabiting fungi reflects a holistic adaptation to challenging ecosystems like poikilohydric, poikilotrophic, and polyextremotolerant. Nutritionally, these fungi are so frugal that mere traces of organic compounds can serve as their sole substrate, generating energy via uncommon catabolisms like PAH (polycyclic aromatic hydrocarbon) degradation. But their survival always rests on extraordinarily low basal metabolic flow, fortified cell walls, compatible solutes, and tightly regulated signaling circuits that together stabilize pH and counteract environmental hostility.

Diversity of fungi associated with rocks and monuments: Fungi associated with rocks exhibit a wide range of taxonomic diversity, encompassing various phyla, including Ascomycota,

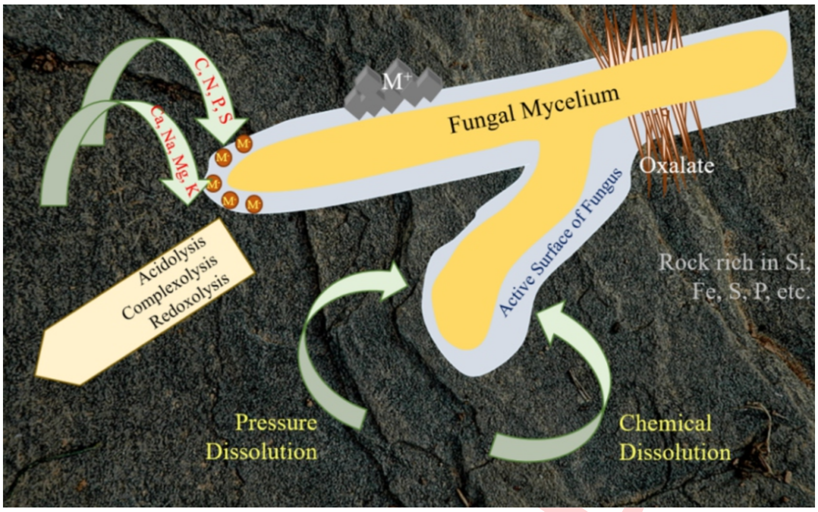


Fig. 3: Ecological roles of monument-associated fungi, highlighting deterioration and discoloration of stone surfaces.

Basidiomycota, and Zygomycota. Among these, Ascomycota is the most prevalent, with lichenized fungi (lichens) forming a significant component. Lichens, symbiotic associations between fungi (mycobionts) and photosynthetic partners (photobionts), are particularly well-adapted to colonizing rock surfaces due to their ability to withstand desiccation, extreme temperatures, and high UV radiation. Non-lichenized fungi also contribute significantly to the fungal diversity on rocks. These include melanized fungi, which possess darkly pigmented cell walls that protect against environmental stressors. Genera such as *Cladosporium, Alternaria* and *Exophiala* are commonly found in rock environments. The diversity of fungi associated with monuments spans multiple taxonomic groups, primarily within the Ascomycota and Basidiomycota phyla. Ascomycota includes a wide range of saprophytic, lichenized, and pathogenic fungi. Common genera found on monuments include *Aspergillus, Penicillium, Cladosporium,* and *Alternaria.* Lichenized fungi, such as those from the genera Lecanora and Caloplaca, form symbiotic relationships with algae or cyanobacteria and are frequently observed on stone surfaces (Table 1). Basidiomycota is represented by wood-decaying fungi that can also colonize wooden components of monuments. Genera such as *Serpula* and *Coniophora* are notorious for causing brown rot and white rot in wooden structures. Zygomycota and Mucoromycota include fast-growing, saprophytic fungi like *Mucor* and *Rhizopus,* which are often found in humid environments on various substrates within monuments.

Ecological functions of fungi associated with rocksand monuments: Fungi associated with rocks perform several crucial ecological functions (Fig. 3). They are primary agents of bioweathering, a process where fungal hyphae penetrate rock surfaces, secrete organic acids, and release mineral nutrients (Burford *et al.,* 2003). This process not only contributes to soil formation but also facilitates the cycling of essential elements such as carbon, nitrogen, and phosphorus. Lichenized fungi play a pivotal role in primary succession on bare rocks, establishing the initial stages of soil development and providing habitats for other organisms. Moreover, fungi associated with rocks can form mutualistic relationships with bacteria and algae, further enhancing their ecological impact (Onofri *et al.,* 2011).

Fungi associated with monuments engage in various ecological functions that influence the deterioration process. Fungi contribute to the physical and chemical deterioration of monuments. They produce organic acids, such as oxalic acid, which can dissolve mineral components of stone, leading to structural weakening. The hyphal growth of fungi can also cause physical disintegration of stone surfaces (Gadd *et al.,* 2024). Many fungi produce pigments that leads to discoloration of surfaces, affecting the aesthetic value of monuments. Melanized fungi, for instance, are known for causing black staining on stone surfaces. Some fungi are involved in biocorrosion processes, particularly on the metal components of monuments. These fungi can produce metabolites that accelerate the corrosion of metals (Burford *et al.,* 2003).

Bioweathering by fungi: Fungi, especially those psychologically and physiologically adapted to rock surfaces (lithobiontic fungi), play a central, mechanistic role in terrestrial biogeochemical cycles, including mineral alteration, organic acid secretion, and biomineral precipitation, *i.e.,* geomycology (Fig. 4) (Bindschedler and Verrecchia, 2022). These rock-adapted fungi frequently include melanized or “black yeast” microcolonial species, e.g., *Exophiala, Coniosporium, Knufia, Aureobasidium,* and crustose lichen photobionts such as *Verrucaria* (Verrucariaceae) that colonize surface and endolithic niches under extreme stress, including heat, desiccation, and oligotrophy through specialized features such as thick pigment-laden cell walls and extracellular polymeric substances (Savković

Table 1: Fungal diversity of rock-inhabiting fungi, along with the kind of colonizing substrate/ rock and the mechanism of bioweathering

Fungal taxon	Substrate	Bioweathering mechanisms	References
Penicillium frequentans	Spanish cathedrals (sandstone, granite, limestone)	Produces oxalic, citric, gluconic acids, cation solubilization; precipitation of calcium/magnesium/ferric oxalates; extensive calcite and silicate dissolutio	Gadd *et al.,* 2024
Aspergillus niger	Tropical and Indian monuments; frescoes, tombs, concrete, plaster	Oxalic, citric acid, acidolyze CaCO$_3$; produces calcium oxalate patinas; chelates Fe^{3+}/Mn^{2+}; hyphal and EPS-mediated microfracturing	Trovão and Portugal, 2021; Biswas *et al.,* 2013
Alternaria alternata	Mural paintings and stone surfaces across European monuments	Demonstrates calcium carbonate dissolution in agar assays; produces a suite of organic acids; pigment excretion, discoloration	Trovão and Portugal, 2021; Ljaljević-Grbić and Vukojević, 2009
Aureobasidium pullulans	Early colonizer on marble/ limestone	Black yeast, melanin rich walls absorb UV; EPS biofilm formation; limited but sustained acid-mediated mineral disruption	Sazanova *et al.,* 2022; Savković *et al.,* 2021
Exophiala spp.	Hypogean walls (Etruscan tombs, catacombs)	Acidogenic filamentous/yeast-like colonies; hyphal penetration into intercrystalline pores with long-term expansion	Gadd *et al.,* 2024; Trovão and Portugal, 2021
Coniosporium spp.	Urban/Mediterranean limestone, marble, granite monuments	Associated with black patina, biopitting, chipping, and exfoliation; forms micrometric crater shaped lesions; colonizes microfissures	Cappitelli *et al.,* 2007
Knufia petricola	Facades of rural granite churches; stone probes	Produces siderophores (iron chelators) to dissolve minerals; penetrates cracks in freshly exposed stone; active biopitting	De Leo *et al.,* 2022; Fuentes *et al.,* 2021
Lecidea auriculata	Alpine and polar siliceous rock exposures	Crustose lichen hyphae bore into silicate grains; lichen mediated exfoliationforms metal oxides	Ljaljević-Grbić *et al.,* 2009
Myriospora smaragdula	Quartzite, granite, and limestone in harsh climates	Hyphal boring into mineral matrix; bioaccumulates Fe and Cu; generates pitting and contributes to fine soil/nutrient accumulation	Ljaljević-Grbić *et al.,* 2009
Fusarium solani	Basalt sculptures in Leizhou "Stone Dogs"	Oxidizes elemental sulfur to sulfuric acid; promotes gypsum crust formation; mechanical and chemical weakening	Wang *et al.,* 2021
Phoma herbarum	Granite and marble surfaces in catacombs and museum walls	Dematiaceous hyphae colonize microfissures; pigment secretion; moderate organic acid release, structural weakening over time	Mascaro *et al.,* 2021
Epicoccum purpurascens	Natural films on sandstone and granite	Produces pigmented aerial mycelia; acidogenic exfoliation of grain cement; contributes to surface erosion; visible biofilm patches	Ljaljević-Grbić *et al.,* 2009

et al., 2021; Sterflinger and Piñar, 2013). On cultural heritage monuments, stones such as limestone, marble, granite, and mortar are colonized by mixed microbial communities wherein dematiaceous fungi exert both aesthetic (pigmentation, black crusts) and structural damage via two principal mechanisms hyphal-tightening, fissure infiltration, biopitting, and secretion of organic acids, CO$_2$ and siderophores that solubilize Ca^{2+}, Fe^{3+}, Mg^{2+} and Al^{3+} from mineral lattices, leading to calcite dissolution and precipitation of secondary minerals such as calcium oxalate or carbonate patinas (Dakal and Cameotra 2012; Gadd *et al.,* 2024). Taxonomically, the fungi most frequently isolated or sequenced from aged monuments across climates via both culture-based and culture-independent approaches include *Cladosporium, Penicillium, Alternaria, Aspergillus, Aureobasidium,* alongside lichenized genera such as *Verrucaria, Caloplaca*, or *Dirina* (Mateus *et al.,* 2024). High-throughput ITS amplicon sequencing and shotgun metagenomics, in combination with scanning/transmission electron microscopy and Clone Library, DGGE fingerprinting, have revealed complex, site-specific consortia including unculturable taxa that often dominate biodeterioration hotspots (Gorbushina *et al.,* 2009). These molecular tools not only illuminate the presence of species but also their functional potential genes for acidogenesis, siderophore synthesis, and stress tolerance, even when microbial load is extremely low or spatially patchy (Gómez-Cornelio *et al.,* 2016; Wu *et al.,* 2023).

Recent work has explored eco-friendly biocontrol agents found to inhibit common bio-deteriogenic fungi (*Penicillium, Cladosporium*) under Petri and simulated stone-surface assays, with comparable efficacy to conventional synthetic biocides but without collateral damage to the substrate or environment (Mateus *et al.,* 2024). Many workers have found that melanin has an immense role in stress tolerance, cell-wall architecture, and gene regulation in bioweathering by fungi. It acts as a powerful quencher of radicals and chelator of metals for biosynthetic pathways such as DHN, DOPA, or pyomelanin, determined by enzymes like laccase, tyrosinase, anchoring to chitin–β–glucan complexes that shape wall structure (Wang *et al.,* 2023). The cell wall integrity and cAMP/PKA signaling modules detect

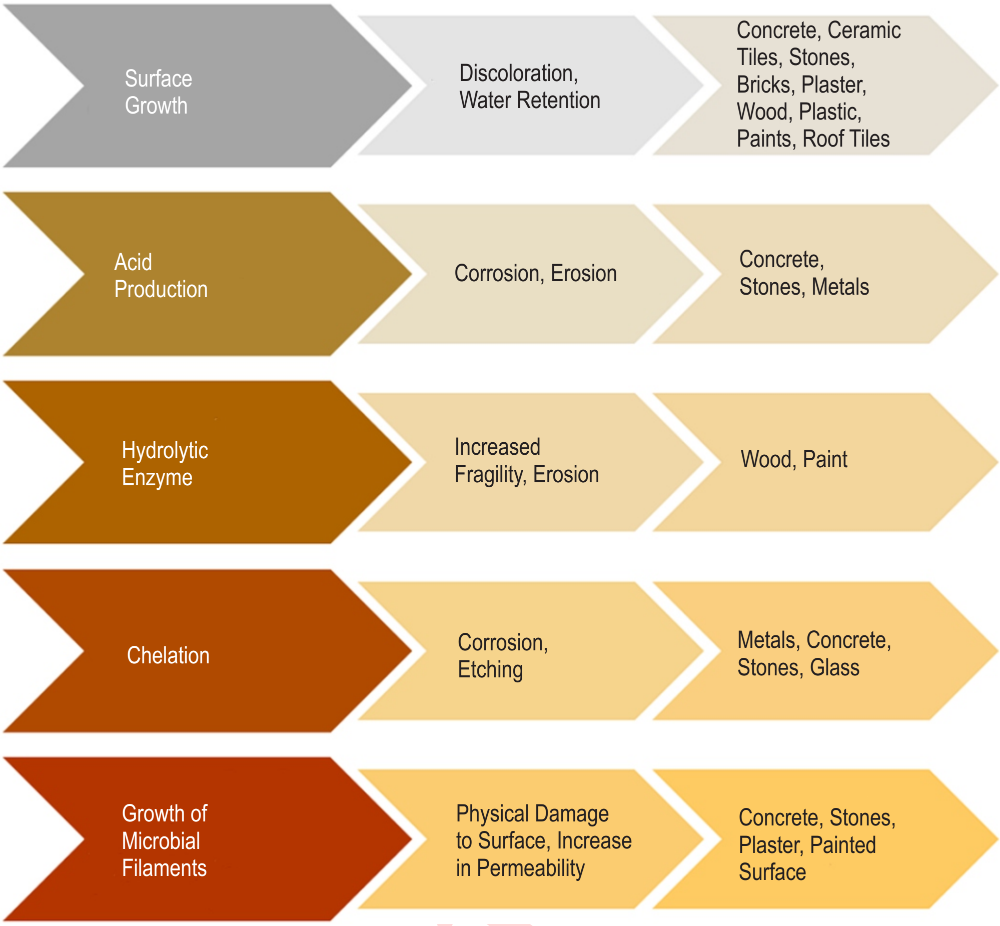


Fig. 4: A diagram depicting various biochemical and physical mechanisms through which fungi contribute to rock weathering.

mechanical or thermal stress, modulate melanin genes, and trigger structural remodeling when disrupted. Reactive oxygen species detoxification relies on enzymes superoxide dismutase, catalase, glutathione peroxidase, peroxiredoxins, and metabolites like glutathione or ergothioneine, all transcriptionally induced under oxidative or heat stress (Nagy *et al.,* 2023). During thermal, osmotic, or cell wall stress, heat shock proteins act as molecular chaperones, directing folding, morphogenesis, and signaling through Hsf1-dependent regulation (Pombeiro-Sponchiado *et al.,* 2017).

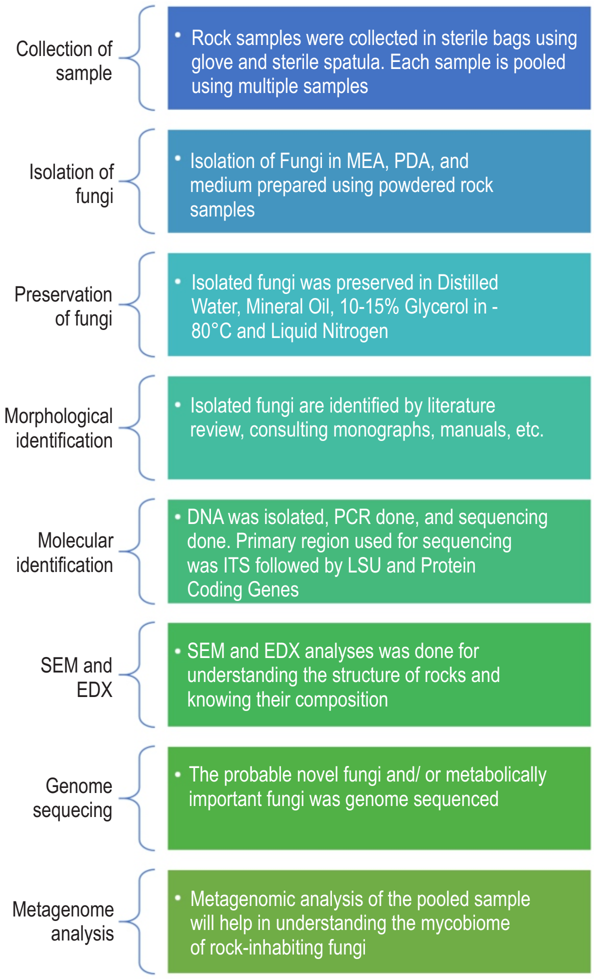
Key regulatory nodes such as Cmr1 upstream of PKS genes coordinate DHN melanin gene clusters and link wall assembly with pigment synthesis (Wang *et al.,* 2023). However, most of this knowledge derives from *in vitro*, clinical, or laboratory systems, not from fungi colonizing natural rock, stone or heritage substrates, and thus *in situ* gene expression under realistic bioweathering conditions remains poorly understood (Schultzhaus *et al.,* 2019). The research focus in the future should target environmental transcriptomics. In this way, it maps the *in situ* regulation of melanin, antioxidant enzymes, heat shock proteins, and wall stress genes in ecologically and anthropogenically exposed sites, including alpine, desert, and lithic ecosystems. Such work will deepen our mechanistic insight into fungal durability and gene expression plasticity during natural biogeochemical cycling under variable field stressors.

Methods used in the study of bioweathering fungi: Studying the diversity of fungi associated with rocks involves a combination of classical and modern techniques. Traditional methods include culturing fungi from rock samples and identifying them based on the morphological characteristics. However, these methods have limitations due to slow growth and low culturability of many rock-associated fungi. However, sampling is an important aspect of these kinds of studies as the selection and identification of correct site is the key to the whole findings (Fig. 5). These techniques provide detailed insights into the interactions between fungi and substrates at micro and nanoscale levels. Studying fungi associated with monuments involves a combination of classical and modern techniques:

Fig. 5: Sampling sites, techniques like swabbing, scraping and micro-sampling.

Classical methods, microscopy and imaging techniques: Traditional culturing techniques involve isolating fungi from rock or soil samples. These methods include plating samples on media to promote fungal growth. Isolated fungi are then identified by morphological characteristics (Hirsch *et al.,* 1995; Sharma *et al.,* 2015; Sharma *et al.,* 2013, 2014; 2016, 2017). Light microscopy and staining techniques are employed to observe the morphological details of fungal spores, hyphae, and reproductive structures. Stains such as lactophenol, cotton blue, and calcofluor white are commonly used to enhance visibility (Burford *et al.,* 2003). Scanning Electron Microscopy (SEM) is used to study the surface morphology and interactions of fungi with rock substrates at high resolution. It provides detailed images of fungal hyphae penetrating rock surfaces, as well as the formation of biofilms and secondary mineral precipitates. Conventional SEM protocols require fixation (by either glutaraldehyde or osmium), dehydration steps, critical point drying, and conductive coatings (e.g. gold or carbon), which induce shrinkage, collapse, and morphological distortion of hyphae and spores, potentially biasing interpretations of bioweathering processes (Drake *et al.,* 2017). Transmission Electron Microscopy (TEM) offers insights into the ultrastructure of fungal cells and their interactions with mineral surfaces at nanoscale. Confocal Laser Scanning Microscopy (CLSM) allows for the three-dimensional visualization of fungal biofilms on rock surfaces. By using fluorescent dyes and markers, researchers can observe the spatial distribution and structural organization of fungal communities *in-situ* (Fomina *et al.,* 2010). Advanced imaging techniques, such as atomic force microscopy (AFM), nano-SIMS (secondary ion mass spectrometry), and 3D laser scanning, can offer detailed insights into the physical interactions between fungi and rock substrates (Fig. 6).

Biochemical and analytical methods: Fungi produce various organic acids, such as oxalic, citric, and gluconic acids, which play a crucial role in the dissolution of minerals. Techniques such as high-performance liquid chromatography (HPLC), mass spectrometry (MS) and ion chromatography (IC)are employed to analyze the metabolic products of fungi, including pigments and organic acids, which contribute to biodeterioration processes. Enzymatic activities of bioweathering fungi, such as cellulases, ligninases, and proteases, are studied using specific substrate-based assays. These enzymes contribute to the degradation of organic matter and the mobilization of nutrients from mineral



Collection of sample
- Rock samples were collected in sterile bags using glove and sterile spatula. Each sample is pooled using multiple samples

Isolation of fungi
- Isolation of Fungi in MEA, PDA, and medium prepared using powdered rock samples

Preservation of fungi
- Isolated fungi was preserved in Distilled Water, Mineral Oil, 10-15% Glycerol in -80°C and Liquid Nitrogen

Morphological identification
- Isolated fungi are identified by literature review, consulting monographs, manuals, etc.

Molecular identification
- DNA was isolated, PCR done, and sequencing done. Primary region used for sequencing was ITS followed by LSU and Protein Coding Genes

SEM and EDX
- SEM and EDX analyses was done for understanding the structure of rocks and knowing their composition

Genome sequcing
- The probable novel fungi and/ or metabolically important fungi was genome sequenced

Metagenome analysis
- Metagenomic analysis of the pooled sample will help in understanding the mycobiome of rock-inhabiting fungi

Fig. 6: A breakdown of techniques for investigating fungal-mediated weathering of rocks, viz., imaging techniques, and chemical analysis methods (EDX, FTIR, Raman spectroscopy).

substrates. X-ray Diffraction (XRD) and Spectroscopy, and various spectroscopy techniques, such as Fourier-transform infrared (FTIR) spectroscopy and Raman spectroscopy, are employed to analyze mineralogical changes induced by fungal activity. These methods provide information on mineral dissolution, secondary mineral formation, and the chemical composition of fungal metabolites (Gadd, 2007).

Molecular techniques: DNA-based methods have revolutionized the identification and study of fungal diversity on monuments. DNA sequencing, particularly high-throughput sequencing technologies, allows for the identification of fungal species directly from environmental samples without the need for culturing. Polymerase chain reaction (PCR) amplification of fungal-specific regions, such as the internal transcribed spacer (ITS) region, followed by sequencing, allows for accurate identification of fungal species (Sharma *et al.,* 2015). Integrating genomics, proteomics, and metabolomics can provide a comprehensive view of the metabolic networks and pathways employed by bioweathering fungi.High-throughput sequencing technologies, such as Illumina and PacBio, enable comprehensive analysis of fungal communities directly from environmental samples without the need for culturing (Ruibal *et al.,* 2009). By applying metagenomics, researchers can analyze the entire genetic material in environmental samples, uncovering the presence of novel fungal species and functional genes involved in weathering processes (Sharma *et al.,* 2024).

Metagenomic data can reveal the presence of genes related to mineral dissolution, organic acid production, and other biogeochemical processes (Fig. 6) (de Menezes *et al.,* 2021). Typical bioinformatics pipelines for such data include quality filtering, chimera removal, OTU clustering (97% identity) or ASV inference, and taxonomic assignment via the UNITE database, often implemented within QIIME or DADA2 workflows (Pec *et al.,* 2017). Metatranscriptomics focuses on sequencing the RNA transcripts in a sample to understand the active metabolic pathways of fungi during bioweathering. It provides information on gene expression and regulatory mechanisms under different environmental conditions (Quemener *et al.,* 2020). Thus, metagenomic and metatranscriptomic analyses provide insights into the functional potential and active metabolic pathways of these fungi in their natural habitats (Voigt *et al.,* 2020).

However, amplicon based high throughput sequencing of fungal communities on platforms like Illumina MiSeq, Ion Torrent or PacBio can overestimate biodiversity because DNA from non viable cells or extracellular fragments persists in environmental substrates, and dead cell DNA may dominate low biomass samples unless RNA based approaches or viability dyes are used (Lindahl, *et al.,* 2013). Despite these caveats, recent studies employing high-throughput sequencing of stone monument biofilms in heritage sites uncovered previously undocumented endolithic fungal taxa and revealed taxon-specific mineral affinities and colonization patterns (Li *et al.,* 2016). Sharma *et al.* (2024) have described in detail various omics technologies adopted for bioweathering and rock-inhabiting fungi.

Environmental and ecological implications: The impact of climate change on bioweathering processes is an important area for future research. Changes in temperature, precipitation patterns, and atmospheric CO_2 levels can influence the fungal activity and their interactions with rock and monument surfaces. Long-term studies and climate modeling can help predict these effects and guide conservation efforts (Liu *et al.,* 2022). Understanding the role of bioweathering fungi in ecosystem functioning and nutrient cycling is crucial for assessing their ecological impact. Future research should investigate how fungal-mediated weathering contributes to soil formation, plant growth, and overall ecosystem health (Galazka *et al.,* 2022). To enhance this section, it is essential to examine the resilience of rock-inhabiting fungi in the face of warming trends, changed humidity, and rising air pollution. Global climate manipulation

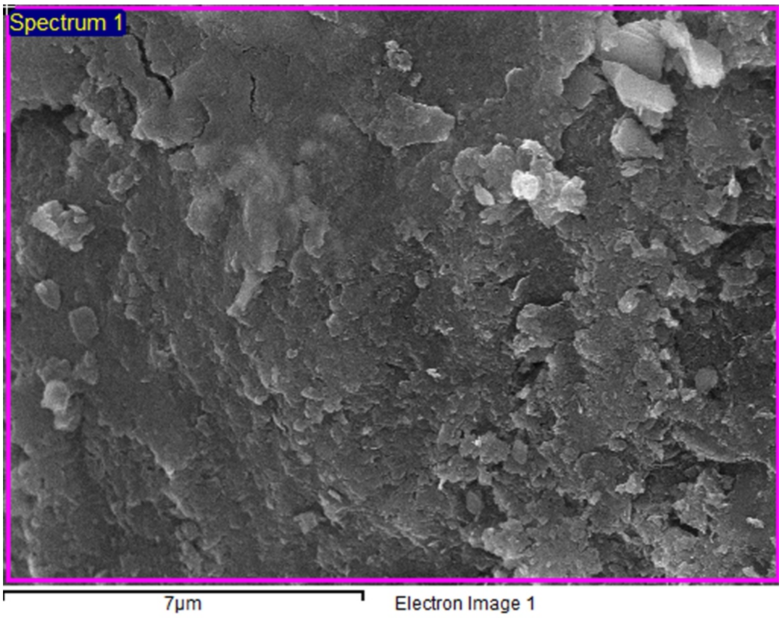


Fig. 7: SEM image of rock sample undergoing bioweathering process.

experiments and climate chamber studies have shown that communities exposed to higher temperatures prolonged desiccation or freeze-thaw cycles, and metal-rich aerosol exposure often suffer reduced fungal biomass, lower soil nutrient immobilization, and shifts toward taxa with thermostable, melanin-enriched cell walls (Finestone *et al.,* 2022). In arid and nutrient-poor alpine or desert ecosystems, what has been termed the "fungal loop" reveals that fungi dominate organic matter mineralization under low water potential and extreme heat, making rock-inhabiting fungi in these environments crucial to nitrogen and phosphorus turnover. Because rock-inhabiting fungi colonize lithic settings with chronic phosphorus and nitrogen limitation, their contribution to biogeochemical cycling in these stress-dominated ecological niches deserve deeper attention.

Furthermore, there is mounting evidence that-melanized rock-inhabiting fungi hyphae and sclerotia resist decay, immobilize metals, and help maintain recalcitrant carbon pools in soil traits directly relevant to bioremediation of pollutants and geological carbon sequestration strategies. The property of melanized rock-inhabiting fungal networks forming stable carbon sinks in weathered rock and the nearby soil environment can lead to large-scale applications for carbon storage. Researchers are exploring exciting facts about rock-inhabiting fungi, *viz.,* whether rising temperatures preferentially favor melanin-rich fungi with enhanced resistance to oxidative stress and whether acid, particulate, or gaseous pollution shifts rock-inhabiting fungal communities toward melanized taxa. Moreover, the climate change in general and heat or pollutant stress systematically selects melanized rock-inhabiting fungi over hyaline fungal morphotypes will clarify long-term ecological impacts and assess the potential utility of rock-inhabiting fungi in climate-resilient biotechnologies under future environmental change.

Impact of bio-weathering by fungi on monuments, cultural heritage and conservation: The presence and activity of fungi on monuments pose significant challenges to conservation efforts. Effective management requires an interdisciplinary approach combining mycology, materials science, and conservation techniques. Strategies for mitigating fungal deterioration include biocides, environmental control, and preventive conservation (Fig. 7). Chemical treatments to control fungal growth, though effective, must be used cautiously to avoid adverse effects on the monument and the surrounding environment. Managing humidity, temperature, and light exposure can reduce fungal colonization and growth. Regular monitoring and maintenance of monuments help to identify and address fungal issues before significant damage occurs (Sterflinger, 2010).

While much is known about the role of fungi in the deterioration of stone and wooden structures, there is still a need for detailed studies on the specific biochemical pathways and environmental conditions that exacerbate this process. Research should aim to identify the environmental factors that promote fungal colonization and growth on monuments, such as humidity, temperature, and pollution levels (Gadd *et al.,* 2024). Developing effective conservation strategies requires a thorough understanding of fungal bioweathering. Future research should focus on creating sustainable and non-toxic biocides and protective coatings that can prevent fungal colonization without damaging the underlying substrates. Additionally, the application of bioremediation techniques, where beneficial microorganisms are used to outcompete harmful fungi, presents a promising avenue for conservation (Onofri *et al.,* 2014). However, the discussion lacks an in-depth examination of numerous limitations and risks associated with various conservation treatments. For example, quaternary ammonium compounds (QACs)-commonly applied antimicrobials-show reduced efficacy against Gram-negative bacteria and biofilm-forming species, and their overuse has been tied to microbial resistance, as well as documented dermal and respiratory irritation and environmental persistence that raise regulatory concerns in jurisdictions worldwide (Arnold *et al.,* 2023). There are many oil-based biocides known for antifungal activity that have the potential to biodegrade. Due to their variable compositions, lack of standard formulations, and substrate incompatibility limit their application in heritage sites (Antoneli *et al.,* 2024). Similarly, UV-blocking nanomaterial coatings can help to protect against harmful sun rays and inhibit microbial colonization. However, these may increase the ecotoxicological risks, aging effects, and altered porosity on the monument surfaces (Gomez-Villalba *et al.,* 2023). There is also an interdisciplinary collaborative research required between mycologists, conservators, and cultural heritage authorities so that efficient protocols can be developed, such as membrane blot, cello-tape methods for proper sampling. This will help in proper mycological analysis without compromising preservation or integrity (Reyes-Estebanez *et al.,* 2018). Moreover, the EU's Biocidal Products Regulation is phasing out persistent synthetic biocides (Ruffolo and La Russa, 2019). Finally, biological indicators of microbial origin can be of great help to detect damage caused to the monuments due to physical, environmental and biological effects (D'Orazio *et al.,* 2024).

Significance, future directions, and conclusion: The biodiversity of rock-inhabiting fungi in nature is well-documented, and their antistress biological characteristics have significant implications for exobiology and ecological functions. Advances in describing rock-inhabiting fungi span morphology, physiology, taxonomy, ecology, evolutionary biology, genomics, molecular biology, and biotechnological applications (Selbmann *et al.,* 2015; Prenafeta-Boldú *et al.,* 2022).The diversity of fungi associated with rocks is vast and encompasses a wide range of taxonomic groups and ecological roles. These fungi are integral to biogeochemical cycles, primary succession, and the maintenance of microbial diversity in extreme environments. Research should continue to explore the functional roles and adaptive mechanisms of rock-associated fungi, contributing to our broader understanding of fungal ecology and evolution.

Fungi associated with monuments exhibit extensive taxonomic diversity and engage in various ecological functions that contribute to the deterioration of cultural heritage sites. Advances in molecular and imaging techniques have enhanced our understanding of these fungi, informing better conservation strategies. Future research should focus on developing sustainable and environmentally friendly methods for managing fungal deterioration, ensuring the long-term preservation of our cultural heritage (Favero-Longo and Viles, 2020). Future research should focus on identification and functional analysis of genes and proteins involved in the secretion of organic acids, siderophores, and other metabolites that facilitate mineral dissolution and nutrient mobilization. Advanced genomic and transcriptomic approaches, such as CRISPR-Cas9 gene editing and RNA sequencing, can provide deeper insights into these processes. Sharma *et al.* (2024) have also reviewed the diversity and mechanisms of fungal mineral interaction through molecular and genomic studies. Bioweathering is a complex process that often involves interactions between fungi and other microorganisms, such as bacteria and archaea. Future studies should investigate these synergistic and antagonistic relationships to understand how microbial communities influence weathering rates and patterns. Metagenomics and microbial co-culture experiments can help elucidate these interactions (Burford *et al.,* 2003).

The study of bioweathering fungi encompasses a diverse array of methods, each offering unique insights into the taxonomy, ecology, and biogeochemical activities of these organisms. Combining classical approaches with advanced molecular, microscopic, and biochemical techniques allows for a comprehensive understanding of fungal bioweathering processes. Continued advancements in these methods will further enhance our knowledge of the ecological roles and environmental impacts of bioweathering fungi (Vasileiou and Summerer, 2020).The future of research on bioweathering fungi related to monuments and rock formations is promising and multifaceted. Advances in molecular biology, high-throughput sequencing, omics technologies, and imaging techniques will enable a deeper understanding of the mechanisms and impacts of fungal bioweathering. This knowledge is essential for developing effective conservation strategies for cultural heritage sites and for understanding the broader ecological roles of these fungi. Continued interdisciplinary research will undoubtedly yield significant insights and innovations in this field.

In conclusion, the authors believe that even though rock-inhabiting fungi are key factors in mineral degradation, there are some critical knowledge gaps, like inadequate taxonomic studies, and many rock-inhabiting fungi are non-sporulating, which makes their identification by morphological parameters difficult. Hence, there is a need to conduct environmental studies on it. Reports on the global fungal diversity of rock-inhabiting fungi, are limited and remained severely unexplored, especially from regions like the Mediterranean, Antarctica, Arctic, Pacific, Africa, and Asia. Since there are few studies, the draft genome of only *Knufia petricola* has been characterized. The authors are also studying the rock-inhabiting fungi of Lameta rock formations and have isolated some new fungi. The drivers of fungal colonization, both environmental and temporal, which affect colonization and bioweathering, are rarely integrated into the ecological models. There is a need to use the transformative opportunities of AI-assisted image analysis integrated with SEM or light microscopy for early detection of degradation by rock-inhabiting fungi. Hence, there is a need to integrate microbiologists, mycologists, conservation scientists, and material engineers within geomicrobiology to study in detail the multigenic/omic profiling and functional assays. Such an integrated framework will allow us not only to map and monitor rock-inhabiting fungi, but also to predict and mitigate biodeterioration of cultural heritage and leverage rock-inhabiting fungi for biomineralization and bio-restoration applications.

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