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The capabilities of bacteria and archaea to alter natural building stones – A review

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Abstract

Microorganisms, including bacteria, archaea, algae and fungi, colonize natural building stones. Bacteria are among the most relevant colonizers, as they impact substrates in multiple forms, primarily attributed to their high diversity. They alter rock properties, induce discoloration, dissolution or precipitation, which can lead to degradation over time or in some cases, protection. Numerous studies suggested a link between rock alteration and bacteria, although there are still inconclusive conclusions. Moreover, the role of archaea remains unresolved. Classical cultivation techniques capture a fraction of bacterial and archaeal diversity. Recently, culture-independent and omics-technologies provide tools to further understand their full diversity and true role. Based on field and experimental work, this comprehensive review provides an overview of biocolonization and potential changes during the 21st Century. To better understand the role of bacteria and archaea, the focus will be on their capabilities to alter natural building stones. It also includes a short overview of methods to understand the processes and dynamics of biocolonization. The conclusions of this work will not only improve our understanding of deterioration in general, but it can also make sustainable biorestoration with bacteria the preferred choice instead of chemical and physical agents.

Keywords: prokaryotes, biodeterioration, bioremediation, building stones, bacteria, archaea

Outline

1. Introduction

Rock and natural stone constitute a relevant portion of the natural and cultural heritage and are a durable part of the built heritage. As a result of atmospheric exposure, the stone properties slowly alter over time, often leading to degradation. It results from a complex interplay between several chemical and physical processes (Siegesmund et al., 2002; Steiger et al., 2011). Besides these abiotic processes, rocks are affected by microorganisms as these are easily colonized by bacteria, archaea, lichens, fungi, protozoa and even small animals or lower and higher plants (Scheerer et al., 2009). This review focuses on bacteria and archaea, which are the simplest unicellular organisms and designated to the prokaryotes. They differ from eukaryotes, such as plants, fungi, animals and green algae, by lacking a nucleus and membrane-defined organelles. Bacteria and archaea have simple cells but differ in composition and structure (Maloy and Hughes, 2013).

Biological colonization of stone substrates can lead to biodeterioration, defined as ‘Any undesirable change in the properties of a material caused by the vital activities of organisms’ (Hueck-Van der Plas, 1968). It is the result of the diverse capabilities of microorganisms and cannot clearly be distinguished from chemical and physical action (Steiger et al., 2011). While the role of many microorganisms in stone alteration was established, Schaffer (1932) addressed an early controversy about the effect of bacteria. This concern was explicitly emphasized by Doehne and Price, 2010 and linked to their assumed relatively low biomass (Hoppert and König, 2006). There have been numerous studies (e.g. Papida et al., 2000; Zanardini et al., 2016) suggesting an important effect of bacteria on building stones. Although, most studies are dispersed, limited in time and samples and focused mainly on bacteria. Combined with the complexity of microbial communities, the high amount of unculturable bacteria and other forms of deterioration, it is hard to determine the true role of bacteria in stone alteration (Gorbushina and Broughton, 2009; Villa et al., 2016).

Moreover, biological colonization can have beneficial effects on building stones (Viles, 2012; Gadd and Dyer, 2017). Colonization can lead to bioprotection, defined as ‘largely passive ways, in which microbial biofilms and plant growth modify conditions at the stone surface to prevent or retard deterioration’ (Viles, 2012). Furthermore, microorganisms and especially bacteria can be applied to restore monuments (De Muynck et al., 2010). They could substitute traditional techniques that have several unwanted side effects, such as possible toxicity, risk of environmental pollution, deterioration, chemical reactivity, etc. However, those traditional techniques are still preferred due to a lack of a complete understanding of microbial communities and the lack of short and long-term monitoring after biological treatment (Romano et al., 2019; Soffritti et al., 2019).

To date, the controversy about bacteria is not resolved, although we know better who is present on building stones and their capabilities to affect stone substrates. Moreover, as most likely, biocolonization will relatively only become more important (McCabe et al., 2011), more efforts are needed to understand their effect. The role of bacteria might be controversial. However, archaea are forgotten, just as in other environments (Bang and Schmitz, 2018). They are still a black box when it is about stone alteration.

To overcome some controversies, this review will give an overview of how bacteria affect natural building stones and induce biodeterioration and bioprotection. It consists of former work that verifies the capabilities of bacteria and includes progress made on archaeal studies. Furthermore, this review will briefly discuss how microorganisms colonize natural building stones (Chapter 2), how they can be studied (Chapter 3) and by which main processes they affect the substrate (Chapter 4). Even though this review focuses on bacteria, more general processes could be induced by multiple organisms, which will be referred to as microorganisms. Chapter 5 will discuss the effect of specific bacteria, divided by their metabolism, while Chapter 6 focuses on archaea. Chapter 7 will give an overview of the effect of pollution on microbial communities in general and what this implies for future colonization. At least, Chapter 8 includes remarks for future work to help to understand the true role of bacteria and archaea and some concluding remarks.

2. Microbial Colonization

Rock surfaces are an extreme habitat exposed to solar radiation, low nutrients, experiencing intense and rapid fluctuations of temperature, water, salinity and pH (Gorbushina, 2007). However, freshly exposed stones are rapidly colonized by bacteria and other microorganisms (Gorbushina and Broughton, 2009). They colonize not only the surface (epilithic growth) but also inside the stones (endolithic growth), for which some microorganisms can actively penetrate the substrate (Valls Del Barrio et al., 2002; Golubić et al., 2015).

Bacteria belong to the primary colonizers of rock surfaces (Gorbushina and Broughton, 2009). The first colonizers are usually identified as autotrophs because they do not need organic material (Rosenberg et al., 2013). Especially cyanobacteria were identified as pioneers due to their resistance to desiccation (Ortega-Calvo et al., 1995; Albertano, 2012). However, even without autotrophs, heterotrophs, which depend on organic material for their growth (Rosenberg et al., 2013), can pioneer by consuming organic material deposited by air pollution or naturally present in sedimentary rocks (Zanardini et al., 2000; Albertano, 2012).

The bacteria rarely live as solitary cells. Instead, they form aggregates of cells embedded in a matrix of extracellular polymeric substances (EPS), defined as biofilms. EPS act as an adhesive layer allowing cells to attach to the substratum. Biofilms are a complex biogenic habitat where different cells communicate, cooperate and compete with each other. Biofilms promote life on rocks as they provide shelter, enhance nutrient accumulation and increase the tolerance and resistance against e.g. desiccation. Furthermore, they establish distinct habitats by introducing gradients in oxygen, nutrients, pH and quorum sensing (Kemmling et al., 2004; Albertano, 2012; Flemming et al., 2016). Biofilm formation and EPS production is extensively attributed to bacteria, although also fungi, algae and archaea can produce EPS (Flemming and Wingender, 2010).

Pohl and Schneider (2002) proposed a colonization protocol on calcareous limestones. At the start, microorganisms will attempt to make the substrate accessible by forming, among others, pits. These pits act as shelter and allow microorganisms to find their ecological optimum location at a specific depth. Hereafter, the microorganisms will form colonies and produce EPS leading eventually to mature biofilms. Hoppert and König (2006) also suggested that fast-growing pioneers are eventually replaced by slower-growing microorganisms. The first phase is regarded as destructive, while mature biofilms should have an overall protective effect, as the colonization of slow growers could only be successful on a stable surface (Pohl and Schneider, 2002; Hoppert et al., 2004; Hoppert and König, 2006).

Not every building stone will experience the same amount of colonization. The potential of colonization depends on the bioreceptivity of the material and the environmental conditions (Guillitte, 1995; Miller et al., 2012), with water availability as the main factor (Ortega-Morales et al., 2004; Ramírez et al., 2010). Guillitte (1995) introduced bioreceptivity as the ability of the material to be colonized by organisms. It is determined by petrophysical properties, including surface roughness, pore space structure and petrochemical characteristics. Miller et al. (2012) gave a detailed review, and overall, rough porous stones are highly susceptible to colonization. Calcareous stones would also be more susceptible compared to siliceous rocks (Miller et al., 2006; Gulotta et al., 2018). Moreover, improvements and clarifications of the concept of bioreceptivity were recently proposed by Sanmartín et al. (2021).

3. Methods to study bacteria and archaea on stones

There are numerous possibilities to study the effect of bacteria and archaea on natural stones. However, both in the field and in the laboratory, an interdisciplinary approach is necessary. The main questions in these kinds of studies are: 1) Which species or groups of microorganisms are present on this stone?; 2) What is the mineralogical content and texture of the natural building stone?; 3) How do they relate to each other and the environment?; 4) Which biological, chemical and physical processes are occurring?; and 5) How can these processes affect the stone characteristics and durability over time?

To answer these questions, it is important to observe bacteria and archaea on the stone surface in their natural habitat and detect biodeterioration features, including biopits and active penetration. This could be performed by microscopy and in particular optical microscopy, scanning electron microscopy (SEM), environmental SEM (ESEM), transmission electron microscopy (TEM) and confocal laser scanning microscopy (Ortega-Calvo et al., 1991; Macedo et al., 2009; Casanova Municchia et al., 2014). Other techniques designed to study the material itself and potential biodeterioration, are among others: X-ray diffraction analysis (XRD), Mercury intrusion porosimetry (MIP), Fourier transform infrared and Mössbauer spectrometry, induction coupled plasma-mass spectrometry (ICP-MS), thermal analysis, Raman spectroscopy, Laser-induced fluorescence, etc. (Dakal and Arora, 2012).

To determine which microorganisms are present, culture-dependent and -independent techniques could be used. For decades, culture-dependent techniques were successfully applied to isolate and identify bacteria colonizing stones. Besides identification, it allows researchers to study their capabilities, such as acid production and calcium carbonate precipitation (Descheemaeker and Swings, 1995; Jroundi et al., 2012) and to test their effect on natural building stones with inducing, among others, discoloration (Ettenauer et al., 2014) and rock dissolution (Frey et al., 2010). A major disadvantage is that most bacteria cannot be isolated (Rappé and Giovannoni, 2003). Other traditional methods estimate microbial activity by measuring specific biomolecules, such as proteins, enzymes, photosynthetic pigments, phospholipid fatty acids (Dakal and Arora, 2012).

More recently, molecular or culture-independent techniques were developed, which can fully describe bacterial diversity. In conservation studies, these included, initially, isolating nucleic acids and phylogenetic analysis (Sanger sequencing of PCR-amplified rRNA genes and cloning) and genetic fingerprinting (e.g. DGGE/TGGE, ARISA, ARDRA, t-RFLP, SSCP). These methods focused mainly on 16S rRNA gene as this is the most common molecular marker for identifying bacteria and archaea (Dakal and Arora, 2012; Otlewska et al., 2014). Although, they could also be applied to functional genes targeting specific groups or metabolism, e.g. for sulfur metabolism (Villa et al., 2015).

Lately, high-throughput techniques referred to the “omics” technologies have drastically changed our views on microbiology. Metagenomics refer to studying all genetic material directly from an environmental sample. Their potential was enhanced by the developments of next-generation sequencing (NGS). Within environmental samples, NGS allows massive in-depth sequencing of DNA without cultivation or cloning (Marvasi et al., 2019; Gutarowska, 2020). The high-throughput analysis of genes (genomics) with NGS was successfully applied to describe bacterial communities on monuments. However, the amount and extent of studies related to their identification on natural building stones remain relatively low. Using high-throughput gene analysis, microbial communities were described across the world on headstones (Brewer and Fierer, 2018) and monuments in, among others, China (Li et al., 2016, 2017; Q. Li et al., 2018), Cambodia (Zhang et al., 2018), Brazil (Gaylarde et al., 2017), Belgium (Schröer et al., 2020b), Italy (Chimienti et al., 2016), Poland (Gutarowska et al., 2015; Adamiak et al., 2018; Dyda et al., 2018) and Portugal (Coelho et al., 2021). Several of these studies used a combined approach with culture-dependent techniques (Li et al., 2017; Dyda et al., 2018; Dias et al., 2020a; Schröer et al., 2020b). Even more recently, MinION nanopore sequencing was developed and applied to cultural heritage. This technique allows rapid species identification and could be applied to study the effect of conservation or cleaning treatments on microbial communities (Grottoli et al., 2020; Pavlovic et al., 2021).

Recent advances also include the high-throughput detection of proteins (proteomics), RNA (transcriptomics) and metabolites (metabolomics). Detailed reviews of all these techniques applied to biodeterioration can be found in Marvasi et al. (2019) and Gutarowska (2020). Metabolomics provide together with proteomics information on biological mechanisms and biomarkers (Gutarowska, 2020). Metabolomic studies are limited to natural building stones. It was applied in a study on building materials in Poland (Gutarowska et al., 2015), rock art in Spain (Roldán et al., 2018) and during a laboratory experiment using halophilic bacteria on bricks, which may be potentially responsible for degradation (Adamiak et al., 2017). An overview figure of the current techniques to study biodeterioration and bioprotection was made by Marvasi et al. (2019) and shown in Figure 1.

Applying new omics technologies and isolating representative bacteria and archaea from natural building stones is a challenging task. Rock substrates are highly complex environments, with surfaces constantly exposed to fluctuating environmental conditions (Gorbushina, 2007). Combined with all heterogeneities of the material itself, this results in numerous micro-niches in which closely related species thrive. Furthermore, the fluctuating environment will favor the growth of species with a high genomic richness to adapt them to oligotrophic and diverse abiotic conditions (Gutleben et al., 2018). The advances in omics technology is complementary to the traditional cultivation of microorganisms. Today, microbial cultivation is still the most solid approach to validate hypotheses raised by omics-technologies (Gutleben et al., 2018).

The described culture-dependent and -independent techniques are optimized for bacteria. Studies on archaea, colonizing building stones are limited. They are overseen due to a lack of standardized detection protocols, primer choice and the difficulty to isolate archaea in pure cultures (Ettenauer et al., 2010; Piñar et al., 2014a; Bang and Schmitz, 2018).

4. Main processes of bacteria and archaea to induce stone alteration

There are numerous possibilities of how bacteria and archaea can affect stone substrates. The main processes will be described below and include the effect of biofilms and EPS (4.1.), biochemical mineral weathering (4.2.), discoloration (4.3.) and calcium carbonate precipitation (4.4.).

4.1. Biofilms and extracellular polymeric substances (EPS)

Microbial biofilms or aggregates of cells embedded in a matrix of extracellular polymeric substances (EPS) are ubiquitous on natural rocks surfaces and include besides bacteria also fungi, algae and lichens (Hoppert et al., 2002; Kemmling et al., 2004; Flemming et al., 2016). Most biomass consists out of EPS, which fills the void between the cell membrane and the surface. It acts as a reactive interface between the microorganisms and rock surface in which compounds, like acids and pigments, excreted by the microorganisms diffuse through and bioleaching, dissolution and discoloration can take place (Hoppert et al., 2002; Sand and Gehrke, 2006; Albertano, 2012). EPS could induce further weathering by binding cations of solubilized minerals (De Philippis and Vincenzini, 1998; Pereira et al., 2009; Rossi et al., 2012a). Papida et al. (2000) noticed during a laboratory experiment accelerated deterioration with bacteria and suggested an important role of EPS. However, EPS could also decrease deterioration as Welch and Vandevivere (1994) showed that depending on the conditions, EPS can dissolve feldspars by complexing ions or inhibit dissolution by irreversibly binding or forming a diffusion-inhibited layer. Moreover, in the field, biofilms cannot always be attributed to increased deterioration (Gulotta et al., 2018) and could even act as a protective layer (de la Rosa et al., 2013). It is also expected that biofilms stabilize the rock surface as long-term colonization is not possible on an intensive degrading surface (Hoppert et al., 2004; Hoppert and König, 2006).

Biofilms could induce patina formation and further discoloration on stones because they contain detritus (dead cells, metabolites), inorganic mineral particles from the material itself and favors the adherence of airborne particles, including pollen, dust, fly ash, aerosols. (Saiz-Jimenez, 1997; Kemmling et al., 2004; Gulotta et al., 2018). Biofilms can also affect the physical properties of building stones, as biofilms seem to buffer temperature variation, reducing thermal stress (McCabe et al., 2015). Furthermore, biofilm formation can change the wettability of minerals from hydrophilic to hydrophobic and vice versa (Polson et al., 2002; Karimi et al., 2012). Hydrophobicity could act as natural waterproofing, reducing water inoculation (Polson et al., 2002). The main effect of biofilms might be on the stone-water relationship. Within building stones, biofilms modify capillary water uptake, alter the water vapor diffusion and decrease the pore water tension (Warscheid, 1996). Extensive studies on the moisture relationship between EPS and rocks are missing, although a similar behavior can be expected in soils. Here, EPS is found to decrease the hydraulic conductivity and water infiltration. It increases the water availability in the top section of soils as it retains moisture and is involved in the uptake of atmospheric humidity and rainwater (Colica et al., 2014). The biofilm could induce clogging of the pore space after water introduction due to swelling of the EPS. This can increase water run-off and reduce water penetration (Malam Issa et al., 2009). However, even within soils uncertainties remain as other authors such as Eldridge (2001) and Rossi et al. (2012b) stated the opposite. They described that EPS increased the hydraulic conductivity and water infiltration by creating micropores, facilitating water movement. Besides affecting the water-stone relationship, Moisture sorption also leads to swelling/contraction of the EPS, which could also cause physical deterioration by introducing mechanical stress. This could play a role in the loosening of mineral grains or rock flakes (May et al., 2003; Büdel et al., 2004; Rossi and De Philippis, 2015).

Overall, biofilms will modify the stone surface. It will most likely increase the wetting periods together with prolonged periods of dampness. This might not only cause further colonization but also affects other forms of weathering induced by water. Increased water exposure could cause prolonged times of mineral dissolution, enhanced freeze-thaw weathering and could affect salt weathering (Siegesmund et al., 2002). McCabe et al. (2015) expected that a biofilm-modified surface would result, due to more difficult evaporation, in water accumulation inside the stone and a deeper wetting front. They suggested that this could facilitate salt transport to depth resulting in future material loss. More research is needed as biofilms might also inhibit water infiltration and the associated weathering (Polson et al., 2002).

4.2. Biochemical mineral weathering

Microorganisms can weather common minerals in natural building stones. Biological rock weathering is essential to release key nutrients. Some bacteria target certain colonize minerals, such as anorthoclase and microcline, containing limiting nutrients such as P and Fe (Rogers and Bennett, 2004).

The relative contribution of bacteria remains poorly understood (Uroz et al., 2009). Bacteria can weather minerals biochemically by oxidation-reduction reactions, acidification and chelating agents. This was determined during multiple experiments, including on phyllosilicates (Hopf et al., 2009; Balland et al., 2010), feldspars (Hutchens et al., 2003; Wang et al., 2018), amphiboles (Kalinowski et al., 2000), carbonates (Orhan et al., 2017) and on rocks such as granites, basalts, trachyte and gneiss (Song et al., 2007; Frey et al., 2010; Štyriaková et al., 2012; Wang et al., 2017). Experiments showed that mineral weathering is more effective when cells are attached as biofilms. Biofilms concentrate dissolution-enhanced metabolites near the mineral surface (Rogers and Bennett, 2004; Frey et al., 2010; Ahmed and Holmström, 2015). Moreover, Papida et al. (2000) suggested that bacterial acid dissolution alone is too weak to induce stone deterioration and participation within biofilms is necessary. The influence of *Paenibacillus* sp. LMG 31982 on a marble surface is illustrated in SM 1B, while SM 1A showed an untreated surface. Here bacterial dissolution created a rough surface with numerous biopits and widened boundaries.

Some bacteria oxidize metals like Fe and Mn, which can lead to extensive solubilization (Benzine et al., 2013; Hansel and Learmnan, 2015; Kappler et al., 2015). Experiments proved that bacteria could oxidize insoluble Fe^{2+} from minerals, including phyllosilicates (Shelobolina et al., 2012; Benzine et al., 2013; Zhao et al., 2017) and pyrite (Bosch et al., 2012; Percak-Dennett et al., 2017). In mainly anaerobic conditions, other bacteria reduce Fe^{3+} and Mn^{4+} (Hansel and Learmnan, 2015; Kappler et al., 2015).

However, acidification is the major mechanism involved in mineral weathering. Bacteria and archaea can produce the strong inorganic acids H_2SO_4 or HNO_3 and the weak acid H_2CO_3. H_2CO_3 is the hydrated form of CO_2 and the main driver of calcium carbonate dissolution and karstification. Bacteria and archaea produce CO_2 due to respiration and can catalyze its hydration by the enzyme carbonic anhydrase inducing further dissolution (Tripp et al., 2001; Li et al., 2007; Bosak et al., 2015). Besides inorganic acids, they also produce organic acids. These acids affect dissolution rates of minerals after changing the equilibrium by decreasing the pH or complexing cations at the mineral surface, but also by affecting the saturation state and speciation of e.g. Al in solution (Drever and Stillings, 1997). Bacteria and archaea can induce further dissolution by producing siderophores. Siderophores are organic molecules that chelate and transport, especially iron, but also other metals to the cell (Ahmed and Holmström, 2014).

On calcareous substrates, one of the microbially produced organic acids: oxalic acid, causes the formation of calcium oxalate films. These are often colored patinas, ranging from ochre to dark brown, covering monuments across the globe, especially in the Mediterranean Basin (Rampazzi, 2019) (SM 2). Oxalate films are regarded as a weathering feature, but due to the low solubility of calcium oxalates compared to calcium carbonates, it can protect the underlying substrate from further erosion and gives historical buildings their typical appearance (Valls Del Barrio et al., 2002; Rampazzi, 2019). Oxalate treatments were even artificially applied to protect marble (Sassoni et al., 2015) or limestone (Cezar, 1998). Its origin on most monuments is questioned, but scientists tend to favor a biological one (Del Monte et al., 1987; Rampazzi, 2019). On building stones, oxalic acid production is mainly attributed to fungi (Gadd et al., 2014), lichens (Chen et al., 2000), or cyanobacteria (Del Monte and Sabbioni, 1983). Other stone-inhabiting bacterial communities are also capable of producing oxalic acid (Di Bonaventura, 1999; Frey et al., 2010). Oxalotrophic bacteria degrade carbon oxalates again, precipitating calcium carbonate (Braissant et al., 2002). Another organic acid, malonic acid, could precipitate as calcium malonate (Salinas-Nolasco et al., 2004), but this has not been extensively found on building stones.

4.3. Discoloration

Microbial discoloration of natural building stones can cause major aesthetic alteration and can be the main reason to remove colonization (Villa et al., 2020). Microbial discoloration might be an acceptable change on some occasions, but some are undesirable. In particular, this is illustrated by headstones, which biocolonization might contribute to the romantic nature of heritage graveyards or might be undesired as for military war graves (SM 3). Bacteria and archaea have been extensively linked to discoloration, mainly induced by pigmentation. Biological pigments are usually stable and retain on the material after cell death (Storme et al., 2015).

Several pigments are related to photosynthetic microorganisms. They produce chlorophyll, carotenoids and phycobiliproteins to harvest light. Chlorophyll is predominantly green and occurs in cyanobacteria, algae and higher plants (Mandal et al., 2020). Carotenoids and phycobiliproteins also protect the cells of extreme light intensity (Mandal et al., 2020). Carotenoids acts as membrane stabilizers to protect them against chemical, osmotic stress and desiccation (Oren, 2009; Köcher and Müller, 2011). Carotenoids are ubiquitously distributed in nature, produced by cyanobacteria, algae, plants and by some other bacteria or archaea. They are red, yellow, orange, brown pigments (Oren, 2009; Köcher and Müller, 2011; Mandal et al., 2020). The carotenoids, essential for photosynthesis, are less common in heterotrophs. However, it is widely distributed within microorganisms living in extreme environments, emphasizing their relevance in protecting the cell. These include salt-loving, halophilic bacteria and archaea, where carotenoids play most likely an important role in salt adaptation (Köcher and Müller, 2011). At least, phycobiliproteins are commonly found in cyanobacteria, some red algae and *Cryptophyta* and have a red or blue color (Mandal et al., 2020).

Besides these pigments mainly used during photosynthesis, other pigments like scytonemin could impact natural building stones. Scytonemin is a yellow-brown pigment from cyanobacteria that acts as a radiation shield protecting the bacterial cells of UV radiation (Sinha and Häder, 2008; Mandal et al., 2020) but also against desiccation and temperature stress (Fleming and Castenholz, 2007). Bacteria can also protect them from UV radiation by producing red to blue gloeocapsins (Storme et al., 2015) or mycosporine-amino acids (MAAs). MAAs are dark brown and widespread and accumulated in organisms exposed to high light intensities. Its role is multifunctional, and MAAs play a role as e.g. antioxidant or against salt, thermal and desiccation stress. They occur in cyanobacteria and possibly in other bacteria, algae, yeasts, fungi and animals (Oren and Gunde-Cimerman, 2007; Kageyama and Waditee-Sirisattha, 2018).

Dark melanins are another important group of pigments, which are most likely the most ubiquitous, resistant, ancient and heterogeneous pigments. They are produced by several bacteria and protects them from environmental stress. Melanins affect bacterial interactions and help survival in extreme environments (Solano, 2014; Pavan et al., 2020).

Besides pigmentation, bacteria and archaea could also indirectly induce discoloration due to their activity by producing organic acids, chelating agents, inducing, among others, mineral precipitation and oxidizing metals. Furthermore, their biofilms and EPS could trap pollutants, pollen, dust,… which could also give rock surfaces a dark appearance (Saiz-Jimenez, 1997; Kemmling et al., 2004; Gulotta et al., 2018).

The induced discoloration will mainly lead to aesthetic alteration, although it also changes the albedo of the rock surfaces and thus the thermal properties. Whereas the biofilm itself tends to buffer surface temperature variations (McCabe et al., 2015), previous experiments suggested that discoloration increases surface temperature and the magnitude of surface topographic change. It indicates that colonization may enhance thermally driven weathering of material by contraction and expansion (Coombes and Naylor, 2012; Mayaud et al., 2014).

4.4. Calcium carbonate precipitation

Besides dissolution, bacteria and archaea affect natural building stones by the process of mineral precipitation. They produce a wide variety of minerals, including carbonates, silicates, phosphates, oxides and sulfides. Precipitation can be biologically controlled or induced as a by-product of their metabolism or growth and is specific for the organism (Ehrlich, 1999; Southam, 2014).

Of all precipitates, calcium carbonate precipitation is spread across almost all bacteria (Boquet et al., 1973) and abundant among stone inhabiting communities. It is induced, among others, by photosynthesis (Dupraz et al., 2009), denitrification (Erşan et al., 2015), urea hydrolysis (Hammes et al., 2003), sulfate reduction (Baumgartner et al., 2006), iron reduction (DeJong et al., 2010), methane oxidation (Luff et al., 2004), degradation of amino-acids (Rodriguez-Navarro et al., 2003), small organic acids and degradation of calcium oxalate (Braissant et al., 2002). The process is governed by the pH, calcium concentration, dissolved inorganic carbon concentration and the availability of nucleation sites. Bacteria induce calcium carbonate precipitation by modifying one of these parameters, mainly by introducing alkalinity through physiological activities (Hammes and Verstraete, 2002). Moreover, their cells act as nucleation sites (Stocks-Fischer et al., 1999), promoting precipitation in general.

Calcium carbonate precipitation affects stone strength and induces cementation, surface protection and crack repair (De Muynck et al., 2010; Ortega-Morales and Gaylarde, 2021), triggering the idea to apply this in stone conservation research. Therefore, it is extensively studied as an environmentally friendly method to remediate building materials. Carbonatogenic bacteria were examined to treat calcareous stones (De Muynck et al., 2011), concrete and cement (De Muynck et al., 2008a, 2008b; Wang et al., 2014). Most studies focused on urea hydrolysis because it can be easily controlled and results in the fastest production of calcium carbonate (De Muynck et al., 2010). However, urea hydrolysis generates polluting ammonium and is inhibited by anaerobic conditions. Therefore, other pathways such as precipitation through denitrification have been studied. Denitrification does not produce toxic by-products and occurs under O_2 limited conditions (Erşan et al., 2015). Stone inhabiting microbial communities can specifically be activated to induce calcium carbonate precipitation. Previous experiments providing culture media on limestone showed the activation of naturally occurring carbonatogenic bacteria for effective consolidation (Jimenez-Lopez et al., 2008; Jroundi et al., 2010, 2020).

Biological precipitation is not always beneficial as the pathway can relate to dissolution elsewhere in the stone. Precipitation could cause preferential metal-ion migration to the surface, leading to 'case hardening' that can temporarily strengthen the rock surface. However, the associated weakening of the substrate will lead to quicker erosion after the case-hardened surface would be lost and thus inducing enhanced biological weathering (Viles and Goudie, 2004; Barrionuevo et al., 2016; Gaylarde et al., 2018).

5. Bacteria colonizing monuments

5.1. Photoautotrophs

Photoautotrophs assimilate complex molecules out of CO_2 using light as an energy source (Rosenberg et al., 2013). Cyanobacteria are by far the most abundant photoautotrophic bacteria on monuments. They are abundant on different lithotypes (Macedo et al., 2009) and can dominate bacterial communities (Gaylarde et al., 2012; Golubić et al., 2015), especially in the tropical and sub-tropical regions (Gaylarde and Gaylarde, 2005). Cyanobacteria colonize almost all illuminated environments, including indoor environments and (artificially) illuminated caves and catacombs, which is undesired (Albertano, 2012; Bruno et al., 2019). They commonly inhabit the surface or hide just underneath, including fissures, cracks and cavities because it provides protection, moisture and mineral nutrients (Friedmann, 1982; Bell, 1993; Walker et al., 2005). Usually, they are patchily distributed due to local inhomogeneities creating micro-environments. Monuments usually harbor different cyanobacterial communities. Tolerant taxa colonize high exposed levels, while less desiccation resistant taxa grow near the ground level, exposed to higher nutrient content and humidity (Albertano, 2012).

Most often, cyanobacterial colonization results in an aesthetic change. The photosynthetic pigments typically cause greenish-yellow, bluish-green or pink/pinkish-orange discoloration (Gaylarde et al., 2012; Prieto et al., 2018). The production of scytonemin causes abundantly dark discoloration (Gaylarde et al., 2007; Cappitelli et al., 2012; Golubić et al., 2015). Cyanobacteria might be the main cause of black patina formation in clean environments (Gaylarde et al., 2007; Cappitelli et al., 2012). Upon monuments, gloeocapsins could lead to dark red discoloration (Stupar et al., 2014) although, its occurrence is not well documented.

Moreover, cyanobacteria are among the main producers of EPS (Rossi and De Philippis, 2015). Their biofilms are known to change the fluid properties inside porous media. Several studies in soils where EPS changed the hydraulic conductivity, induced bioclogging and absorbed water from the atmosphere belonged to cyanobacterial biofilms (Malam Issa et al., 2009; Rossi et al., 2012b; Colica et al., 2014). Their EPS filaments were also linked to physical deterioration due to swelling after hydration (Belnap and Gardner, 1993; Rossi and De Philippis, 2015).

Cyanobacteria also play an essential role in calcium carbonate precipitation. Their photosynthetic activity increases the pH by consuming CO_2 and HCO_3^-, while the produced EPS acts as binding sites of the Ca^{2+} and CO_3^{2-} (Danin and Caneva, 1990; Albertano et al., 2000; Ortega-Morales et al., 2000; Dittrich and Sibler, 2010). Moreover, Büdel et al. (2004) reported a pH increase to 9.5 – 10.5 after alkalization induced by cyanobacteria. This can weather sandstone by solubilizing silica, causing a special type of "exfoliation". They could also be involved in gypsum precipitation as Gaylarde et al. (2017) and Braithwaite and Whitton (1987) detected neo-formed gypsum crystals around cyanobacterial filaments. Gypsum becomes less soluble at higher pH, which is expected near phototrophs during photosynthesis. Heterotrophs could dissolve gypsum during the night by acid production, while during the day, cyanobacteria could redeposit the gypsum around their cells. Such recrystallization cycles could lead to larger gypsum crystals and disrupt the stone (Gaylarde et al., 2017).

Cyanobacteria are not known to produce significant amounts of acids. Although, some members, such as *Chroococcus lithophilus*, penetrate calcareous stone till 2 mm deep by creating depressions, perforations and tunnels (Golubic et al., 2000; Golubić et al., 2015). Furthermore, some studies revealed the occurrence of chelating uronic acids and sulfated groups in EPS from cyanobacteria (Bellezza and Albertano, 2003; Bellezza et al., 2006; Rossi and De Philippis, 2015).

5.2. Chemolithotrophic bacteria

Chemolithotrophs are specialized to oxidize inorganic compounds as an energy source. These include methane, ammonia, nitrite, sulfur compounds, hydrogen, iron, manganese. Most are chemolithoautotrophic as they also use CO_2 as a carbon source. Some bacteria are facultative autotrophs who can switch between autotrophy and heterotrophy (Hooper and DiSpirito, 2013). On rocks, especially members that oxidize sulfur, nitrogen, iron and manganese, can have an impact.

5.2.1 Sulfur and nitrogen oxidizing bacteria

Chemolithoautotrophic sulfur and nitrogen oxidizing bacteria are rare on monuments. 16S rRNA Next-Generation Sequencing detected across the world only the absence (Chimienti et al., 2016) or low amounts of chemolithoautotrophic bacteria (Li et al., 2016; Schröer et al., 2020b). However, they are strongly linked to the deterioration of several building stones, including limestone (Mitchell and Gu, 2000), marble (Bartolini and Monte, 2000) and sandstone (Meincke et al., 1989; Mansch and Bock, 1998; Li et al., 2008; Kusumi et al., 2011).

Nitrifying bacteria are the most common, especially underneath the stone surface (Meincke et al., 1989; Mansch and Bock, 1998). However, colonization takes several years; they have a slow growth rate and require high moisture content suggesting a limiting role in extreme climates (Mansch and Bock, 1996, 1998; Bock and Wagner, 2006). They constitute out of ammonia-oxidizing bacteria (AOB) and nitrite-oxidizing bacteria (NOB). AOB gain energy by oxidizing ammonia to nitrite and NOB grow by oxidizing nitrite to nitrate. It results in the production of nitric and nitrous acid (Bock and Wagner, 2006). Nitrous and nitric acid may dissolve minerals such as calcium carbonate and can lead to an enrichment of nitrate salts (Wolters et al., 1988). However, a relationship between the nitrate content of stone material and the number of nitrifying bacteria could not be established (Mansch and Bock, 1998). According to Urzi and Krumbein (1994), the activity of nitrifying bacteria changes the stone's properties. It increases the porosity, induces exfoliation and powders the stones. Mansch and Bock (1996) showed, under optimal conditions, the potential of nitrifying bacteria to deteriorate natural sandstones in a simulated smog atmosphere. Nitrifying biofilms promoted gypsum crust formation, and biological nitric acid was eight times stronger in corroding the material compared to chemical corrosion.

Sulfur oxidizers can oxidize reduced sulfur compounds: elemental sulfur, thiosulfate or sulfides. It results in the production of sulfuric acid (Muyzer et al., 2013). Sulfur oxidizers were rarely detected on historical buildings, probably due to the low amount of reduced sulfur components in the atmosphere (Mansch and Bock, 1998). However, biogenic sulfuric acid is the main cause of concrete deterioration in sewer systems and water treatment plants (Milde et al., 1983; Okabe et al., 2007). Moreover, sulfuric acid may dissolve calcium carbonate and other minerals resulting in gypsum crust formation (Rodriguez-Navarro and Sebastian, 1996). Gypsum crusts are sulfate encrustations with often a black appearance due to the incorporation of particulate matter or airborne dust (Camuffo et al., 1983). Sand and Bock (1991) demonstrated the potential of sulfur oxidizers and several *Thiobacilli* (now reclassified to *Acidithiobacillus*, *Halothiobacillus*, *Thiomonas, Starkeya,…*) (Moreira and Amils, 1997; Kelly and Wood, 2000; Kelly et al., 2000) to deteriorate concrete by sulfuric acid. A laboratory experiment with the sulfur oxidizer *Acidothiobacillus thiooxidans* resulted in material loss and gypsum formation on limestone and concrete (De Graef et al., 2005). Anoxygenic phototrophic sulfur bacteria were detected on building stones as well (Villa et al., 2015), but their influence on stone deterioration remains unknown. Some members are known to precipitate $CaCO_3$ (Bundeleva et al., 2012).

The occurrence of both nitrifying and sulfur-oxidizing bacteria is positively correlated with air pollution (Mansch and Bock, 1998; Villa et al., 2015; Li et al., 2016; Schröer et al., 2020b). Ammonia mainly originates from agriculture, while NO_x and SO_2 are primarily from fuel combustion from e.g. traffic and industry (Hoesly et al., 2018). Those pollutants seem to be fertilizers for chemoautotrophs but are also an important source of stone decay. Doehne and Price (2010) questioned how airborne SO_2 and NO_x are oxidized to sulfuric and nitric acid and if bacteria play a role in it. This question remains unresolved, but low abundances or absence, even on gypsum crusts (Schröer et al., 2020b), combined with slow growth, suggests the domination of chemical processes.

5.2.2. Metal-oxidizing bacteria

Some bacteria oxidize metals such as Fe or Mn, elements common in rocks and natural building stones. Several bacteria oxidize Fe^{2+} as an energy source (Kappler et al., 2015), while it is unknown why some bacteria oxidize Mn (Hansel and Learmnan, 2015). Oxidation and preferential migration of these metals cause discoloration but could also alter the surface by the patina formation and case hardening (McAlister et al., 2003). These patinas can act as a protective layer (Valls del Barrio et al., 2002) but could also weaken the inner stone and change the water retention, similar to biofilms (McAlister et al., 2003; McCabe et al., 2015). Iron-rich stains were frequently identified on marbles (Bams and Dewaele, 2007), sandstones (McAlister et al., 2003) and limestones (De Kock et al., 2017). In the past, just as all iron redox reactions, this was related to abiotic factors like atmospheric weathering (De Kock et al., 2017). Although, now it is known that iron redox reactions can be biologically mediated (Melton et al., 2014). Dias et al. (2019) and Valls Del Barrio et al. (2002) suggested biological Fe^{2+} oxidation and precipitation on building stones or sculptures, but clear evidence is missing. These iron-rich patinas resemble iron films found on natural stones worldwide, but also here there is no agreement on its origin. Bacteria and iron-oxidizers, in particular, are suspected to play an important role (Dorn, 1998).

Besides Fe^{2+} oxidation, Mn^{2+} oxidation is widespread. This ability was found in several bacterial phyla but also occurs within two fungal phyla (Hansel and Learmnan, 2015). The role of Mn-oxidizing bacteria in stone deterioration remains unclear. The Mn-enriched crust can be present on monuments, especially when constructed with siliceous stones, such as quartz-based sandstone (SM 4A and SM 4B) (Macholdt et al., 2017). Some authors suggested a biogenic origin (Uchida et al., 2016; Vicenzi et al., 2016; Sharps et al., 2020), while others propose an abiotic one (Macholdt et al., 2017). In both cases, clear evidence is missing, but faster growth rates of the crust favor a biotic origin (Sharps et al., 2020). Mn-crusts resemble rock varnish, which are often found in deserts (SM 4C and SM 4D), but questions remain about their origin. There are several hypotheses, including biotic, abiotic and mixed origin (Dorn, 2008). Dorn and Oberlander (1981) and Krumbein and Jens (1981) confirmed a potential biogenic origin after the growth of rock varnish in the laboratory after applying bacteria, fungi and cyanobacteria. Furthermore, Northup et al. (2010) detected several bacteria able to oxidize Mn on rock varnish. In other natural environments such as streams and caves, Mn crusts were found as well, and Saiz-Jimenez et al. (2012) and Tani et al. (2003) attributed this to a biological origin by bacteria and fungi. These crusts and stains can be deleterious in caves as it endangers pre-historic rock art (Saiz-Jimenez et al., 2012).

Moreover, bacteria can oxidize other metals, such as lead. Lead oxidation can cause red discoloration (e.g. on marble) due to the presence of a mimium (PbO_4) (Realini et al., 2005; Cantisani et al., 2019). There are several hypotheses about the origin of this discoloration, but Realini et al. (2005) linked this to the bacterial oxidation of lead.

5.3. Chemoorganotrophic bacteria

Chemoorganotrophs are heterotrophs and need organic compounds for energy generation and carbon source (Rosenberg et al., 2013). They frequently occur on natural buildings stones, with a high diversity and are often dominating (Schröer et al., 2020b; Zanardini et al., 2016).

They can use several types of organic substrates retrieved by autotrophs, but also by dust or pollution. Our knowledge about the effect of heterotrophic bacteria on natural building stones is limited. They mainly affect stone monuments by discoloration due to pigmentation and by the production of organic acids and siderophores. Studies discussing mineral weathering in soils showed heterotrophic bacteria playing an essential role in releasing nutrients (Uroz et al., 2009). Isolation campaigns from monuments resulted that often only a low fraction of the isolates produced acids able to dissolve calcium carbonate (Descheemaeker and Swings, 1995; Abdulla et al., 2008; Schröer et al., 2020b). However, most laboratory experiments of bacteria deteriorating minerals involved heterotrophic bacteria (Balland et al., 2010; Hopf et al., 2009; Hutchens et al., 2003; Kalinowski et al., 2000; Orhan et al., 2017; Wang et al., 2018).

Heterotrophic growth leads abundantly to carbonate precipitation (Boquet et al., 1973). Calcium carbonate precipitating bacteria have been isolated on monuments worldwide (Urzi et al., 1999; Jroundi et al., 2010; López-Moreno et al., 2014; Andrei et al., 2017; Montaño-Salazar et al., 2018; Q. Li et al., 2018; Andreolli et al., 2020). At some locations, carbonatogenic bacteria constituted more than half of all isolates (Urzi et al., 1999; Jroundi et al., 2010; Q. Li et al., 2018). Often they belong to the genus *Bacillus* or *Pseudomonas* (Andrei et al., 2017; Q. Li et al., 2018). Moreover, mainly chemoorganotrophs were studied to restore building stones (De Muynck et al., 2010). It is also this community, which can be activated on building stones to start in-situ precipitation (Jimenez-Lopez et al., 2008; Jroundi et al., 2010). Calcium precipitation by chemoorganotrophs, without specific stimulation, is not well documented. However, Li et al. (2018) linked microbially induced calcium carbonate precipitation by *Crossiella* to aesthetic deterioration in the form of white plaques covering building stones. Besides restoring monuments by calcium carbonate precipitation, other members could clean buildings and remove organic pollutants (Parulekar-Berde et al., 2020), including graffiti (Bosch-Roig et al., 2021).

Chemoorganotrophs can also induce discoloration. Isolation campaigns resulted that the majority of these bacteria on stones produced yellow, red, orange or other pigments (Suihko et al., 2007; Abdulla et al., 2008; Schröer et al., 2020b). By producing melanins, chemoorganotrophs like *Streptomyces*, were attributed to black or brown discoloration on monuments and wall paintings (Abdel-Haliem et al., 2013; Sakr et al., 2020).

The most occurring chemoorganotrophs belong to the Actinobacteria, Proteobacteria, Firmicutes, but also Chloroflexi and Deionococcus-Thermus occur abundantly. Actinobacteria often dominate the microbial community on building stones (Chimienti et al., 2016; Schröer et al., 2020b). They are well adapted to survive the extreme environment of a rock substrate and can resist desiccation, UV radiation and salinity (Bull, 2011). Several Actinobacteria are known to produce hyphae-like structures (Barka et al., 2016). These can penetrate building stones and increase the surface area of biofilm formation (May et al., 2003). Abundant genera are *Arthrobacter*, *Rubrobacter* and members of the *Geodermatophilaceae* (*Blastococcus*, *Modestobacter* and *Geodermatophilus*). These groups have been extensively linked to different kinds of stone deterioration and remediation. *Rubrobacter* and *Arthrobacter* could cause red discoloration of monuments (Schröer et al., 2020b, 2020a) and especially of salt-attacked walls (Piñar et al., 2014a). *Arthrobacter* could also play an important role in calcium carbonate precipitation (Cacchio et al., 2003; Montaño-Salazar et al., 2018). *Geodermatophilaceae* at least was suggested to contribute deterioration by colored patina formation, bio-pitting and powdering (Urzi et al., 2001).

5.4. Halophilic bacteria

Soluble salts are common secondary minerals found in built heritage. They are considered one of the main actors in the degradation of stone walls and mural paintings (Charola, 2000; Doehne, 2002). Salt-loaded substrates form a habitat for moderate halophilic to extreme salt-tolerant bacteria and archaea, mainly chemoorganotrophs. Halophilic bacteria commonly produce carotenoid pigments such as bacterioruberin and salinxanthin (Oren, 2009; Jehlička et al., 2013) and cause rosy or pink discoloration patterns on stones (SM 5). Piñar et al. (2014) reviewed this phenomenon in detail. The bacteria inhabiting this habitat are similar on several monuments across Europe and frequently co-occur with archaea. Bacterial isolations performed on salt-attacked monuments, in general, resulted in strains from yellow to pink or purple. Most isolates belonged to Firmicutes, especially to the genus *Halobacillus* and *Bacillus* (Ettenauer et al., 2014) and to Gammaproteobacteria with among others *Halomonas* (Piñar et al., 2014b). Raman spectroscopy confirmed a bacterial origin of pink discoloration on mural paintings by comparing carotenoid pigments from two isolated *Halobacillus* strains and in-situ measurements (Cojoc et al., 2019). A similar approach linked *Arthrobacter agilis* to rosy discoloration (Tescari et al., 2018b, 2018a). *Arthrobacter agilis* is also known to produce bacterioruberin (Fong et al., 2001). Overall, pink patinas are linked to salt efflorescence, although pink discoloration might also develop without a high salt content (Tescari et al., 2018a; Schröer et al., 2020b).

Culture-independent techniques indicated a relationship between the rosy discoloration and massive occurrence of Actinobacteria, with *Rubrobacter* often as the dominant genus. Members of this genus, such as *Rubrobacter radiotolerans*, contain the carotenoids bacterioruberin and monoanhydrobacterioruberin (Saito et al., 1994; Imperi et al., 2007). *Rubrobacter* could also play an active role in deterioration, salt efflorescence and mineral precipitation. *Rubrobacter* strains isolated from weathered monuments penetrated through the porous rocks, detached mineral grains, and could precipitate the salt struvite ($MgNH_4PO_4.6H_2O$) out of culture medium and on rock samples (Laiz et al., 2009).

Besides identifying pigments, other experiments confirmed the discoloration of building stones induced by halophilic bacteria. Ettenauer et al. (2014) induced rosy discoloration on gypsum plaster and Hontoria limestone after incubating two isolated strains: *Halobacillus naozhouensis* and *Kocuria polaris*. Moreover, the isolates caused active dissolution as Field-Emission Scanning Electron Microscopy (FESEM) revealed etched gypsum crystals and cavities in the substratum. Schröer et al. (2020a) discolored Savonnières limestone after applying *Arthrobacter agilis* during a water run-off test.

5.5. Anaerobic pathways

The role of anaerobic respiration and fermentation of bacteria on monuments is unclear. The surface of natural building stones is exposed to oxygen, which should impede or discourage anaerobic metabolism. However, high stone moisture can proved suitable environmental conditions for anaerobic or microaerophilic conditions (Mansch and Bock, 1998). Furthermore, already a few millimeters underneath the surface, oxygen levels can decrease rapidly, as pointed out by measurements from sediments accumulated in the Altamira cave by Portillo and Gonzalez (2009). Such oxygen profiles also exist in biofilms where aerobic zones of tens to a few hundred micrometers are often reported (Stewart and Franklin, 2008).

In the absence of oxygen, several bacteria start reducing nitrate to nitrite and nitrogen gas (Shapleigh, 2013). Mansch and Bock (1998) revealed the denitrifying potential of stone inhabiting microbial communities. However, an isolation campaign by Schröer et al. (2020b) did not result in significant growth of denitrifiers. Their growth and occurrence can be beneficial for rock substrates. Denitrifying bacteria have been applied to remove nitrate salts from monuments and wall paintings (Alfano et al., 2011; Bosch-Roig et al., 2013; Romano et al., 2019). Moreover, they can induce calcium carbonate precipitation (Erşan et al., 2015).

Another important group is the sulfate-reducing bacteria (SRB), which reduce sulfate (SO_4^{2-}) to sulfide (H_2S, HS^-). For a long time, the misunderstanding existed that SRB were strictly anaerobic. Although, several members tolerate oxygen and grow and survive in microaerophilic conditions (Baumgartner et al., 2006; Rabus et al., 2006). SRB are known degraders of iron and steel (Muyzer and Stams, 2008). Deterioration of natural building stones by SRB is obscure, but Portillo and Gonzalez (2009) found a high diversity of SRB in the Altamira cave and expected a potentially negative effect on rock paintings. SRB are detected on building stones by Schröer et al. (2020b) and Villa et al. (2015). SRB can be beneficial as they were successfully applied to remove black gypsum crusts on historical buildings (Cappitelli et al., 2006; Alfano et al., 2011). They could also induce darkening due to the reaction of sulfides with metals (Portillo and Gonzalez, 2009), precipitating sulfides, especially pyrite (FeS) with the occurrence of iron (Rabus et al., 2006), but also sphalerite (ZnS) (Labrenz, 2000). Furthermore, SRB are regarded as key players in calcium carbonate precipitation, even in the aerobic zones (Baumgartner et al., 2006). They could also play a role in dolomite precipitation. This is not known as a serious problem on natural building stones, but newly formed dolomite in surface crusts was found on limestones (Rodríguez-Navarro et al., 1997), marbles (Monte and Sabbioni, 1980) and dolostones (Valls Del Barrio et al., 2002). There is still a high controversy about dolomite formation, referred to as the 'dolomite problem'. At low temperatures, dolomite precipitation was only demonstrated by bacteria and mainly with SRB (Vasconcelos et al., 1995; Krause et al., 2012) or organic molecules such as EPS (Bontognali et al., 2014).

During anaerobic conditions, some bacteria can also change the redox state of metals such as Fe^{3+} and Mn^{4+}. (Hansel and Learmnan, 2015; Kappler et al., 2015). Furthermore, Fe^{2+} oxidation could also anaerobically occur when coupled e.g. with denitrification. Experiments evidenced that anaerobic Fe^{3+} reduction and anaerobic Fe^{2+} oxidation change the redox of structural Fe in minerals like phyllosilicates (Benzine et al., 2013).

Besides respiration, several bacteria can ferment organic substrates, producing, among others, alcohols and acids (Rosenberg et al., 2013). These metabolites could deteriorate natural building stones, but there is no sign that this happens on a large scale forming a serious issue.

6. Archaea

Initially regarded as extremophiles, archaea are abundant and ubiquitous (Cavicchioli, 2011; Adam et al., 2017; Bang and Schmitz, 2018). Archaea have been overlooked, and their role in stone alteration remains unknown. Although, they can play a role in biodeterioration, such as *Halobacterium salinarum,* seen as a starting actor on parchment discoloration and degradation (Migliore et al., 2019).

Some members were identified especially on salt-attacked, rosy-discolored walls and mural paintings in Austria (Rölleke et al., 1998; Piñar, 2001; Piñar et al., 2009, 2014a; Ettenauer et al., 2010, 2014), Italy (Imperi et al., 2007) and Spain (Piñar, 2001). They belonged to extreme halophilic genera within the Halobacteriales. Most halophilic archaea produce high amounts of carotenoids (including bacterioruberin) in their cell membrane, leading to pink-red colors. Archaeal bacterioruberin pigments are generally the main cause of the typical red color of brines (Oren, 2009). However, in stones, archaea were mainly detected in a low abundance, such as < 0.1 % detected by Imperi et al. (2007). For this reason, a causative link with rosy discoloration has not been established. Furthermore, halophilic archaea were detected on exfoliated sandstone (Lan et al., 2010; Zanardini et al., 2016), carbonates (Chimienti et al., 2016; Coelho et al., 2021), bricks (Adamiak et al., 2018) and even painted walls (Ogawa et al., 2017), but all containing low diversity and abundance. At some locations, these were accompanied by Crenarcheota (Lan et al., 2010; Ogawa et al., 2017; Adamiak et al., 2018) and Parvachaeota (Adamiak et al., 2018). The origin of halophilic archaea in stones might be in the ocean in which the sediments were deposited. Archaea represent almost a third of all prokaryotic cells in the ocean (Karner et al., 2001; Herndl et al., 2005). Meier et al. (2017) detected archaea inside the German Triassic Muschelkalk and suggested it as a relic of the Tethys Sea. Furthermore, McGenity et al. (2000) and Piñar et al. (2009) suggested that halophilic archaea found in ancient salt deposits might be the remnants of archaea inhabiting hypersaline seas (McGenity et al., 2000; Piñar et al., 2009).

Moreover, chemolithoautotrophic archaea produce just like their bacterial counterparts' inorganic acids (HNO_3 and H_2SO_4). Their occurrence is still obscure, but they were detected on sand- (Meng et al., 2016, 2017) and limestones (Coelho et al., 2021). Ammonia-oxidizing archaea (AOA) might be more important than previously thought. Recent studies focusing on the amoA gene on deteriorated sandstone temples in Cambodia revealed a higher abundance and diversity of AOA compared to ammonia-oxidizing bacteria (AOB) (Meng et al., 2016, 2017). This dominance is also found in the marine and soil environment, in which AOA could be favored due to low ammonia concentrations (Hatzenpichler, 2012). 16S rRNA gene sequencing also detected AOA within sandstone temples (Zhang et al., 2018) and on deteriorated sandy limestone (Schröer et al., 2020b). So far, sulfur-oxidizing archaea were not detected on stone monuments.

At least, methane-producing (methanogens) and methane-oxidizing prokaryotes (methanotrophs) are remarkable components of stone microbial communities. Methanogens are strictly anaerobic archaea, while methanotrophs can be bacteria or archaea, which oxidize methane both aerobic or anaerobically (Whitman et al., 2014; Costa et al., 2019). Kussmaul et al. (1998) detected methanogens and accompanied methanotrophs in different building stones, including sandstone, limestone and marble. Methanotrophs co-occurred almost always with methanogens, suggesting that methanotrophs depend on biogenic methane production. They were only found in very low abundances (CFU < 100 per gram rock), so their effect will be minimal. However, methanogenic activity can induce calcium carbonate (Budai et al., 2002) and dolomite precipitation (Roberts et al., 2004).

7. Future colonization and stone deterioration

The environmental change during the 21st Century poses severe threats for our heritage. Biological communities on building stone and the induced biodeterioration will alter due to changing environmental conditions with as key factors climate and atmospheric chemistry (Viles and Cutler, 2012).

In the past, air pollution was one of the main actors enhancing stone deterioration. Mainly SO_2 can negatively impact stone substrates inducing black gypsum crust formation on calcareous stones (Camuffo et al., 1983; Bonazza et al., 2007). Overall, its effect is diminishing as SO_2 emissions decreased sharply, especially within Europe, North America and China, while in other regions such as India, it recently increased (Aas et al., 2019). SO_2 would inhibit microbial colonization (Smith et al., 2011; Viles and Cutler, 2012). Other forms of pollution might fertilize the substrate with carbon, promoting and sustaining heterotrophic growth, even before initial autotrophic growth (Saiz-Jimenez, 1993; Zanardini et al., 2000). Nitrous oxides (NO_x) related to traffic emissions might enhance microbial growth removing nitrogen limitations on the substrate (Smith et al., 2011; Viles and Cutler, 2012). Just as SO_2, NO_x decreased recently in the industrialized world (Huang et al., 2017) but with a slower rate compared to SO_2. Improved air quality and a shift in pollution regime might increase future biological diversity and the relative effect of biodeterioration. The effect of air pollution on bacteria and archaea is complex. Mitchell and Gu (2000), Ortega-Morales et al. (2019) and Zanardini et al. (2000) confirm the reduced biodiversity by air pollution using traditional microbial methods. Studies using culture-independent techniques by Schröer et al. (2020b) and Villa et al. (2015) detected in polluted urban environments, a higher diversity of specialized bacteria and archaea such as sulfur oxidizers, SRB, AOA and AOB, even in the occurrence of higher SO_2 levels (Villa et al., 2015). The reduced biodiversity detected by culture-dependent techniques might be related to the difficulties of culturing these specialized bacteria and archaea. This is also suggested by an isolation campaign of Schröer et al. (2020b), which resulted in a lower diversity in the urban environment.

The improved air quality will have a significant effect on the aesthetics. During high SO_2 levels, buildings were covered by black gypsum crusts. Reduced pollution will create other forms of discoloration such as "yellowing" (Grossi et al., 2007) but also biological induced discoloration including "greening" due to algae (SM 6) (McCabe et al., 2011), "reddening" by heterotrophic bacteria (Schröer et al., 2020b) or "greying" by cyanobacteria (Gaylarde et al., 2007).

Furthermore, climate change will influence colonization. Increased CO_2 emissions theoretically promote photosynthetic growth, but on monuments, other nutrients and moisture are probably limiting (Viles and Cutler, 2012; Prieto et al., 2020). The overall increased temperature should enhance biological activity but could cause drier conditions. Changes in precipitation might be the most relevant factor as moisture shortage often limits biological colonization. The main factor will be the period of wetting instead of the absolute quantity of precipitation. Available moisture will likely decrease as extreme weather and rain events will become more frequent because large parts of the rain will run off (Viles and Cutler, 2012; Orr et al., 2018). However, large floods could cause events of extraordinary humidity (Haugen and Mattsson, 2011). Mathematical models about biomass accumulation within Europe at the end of the 21st Century by Gómez-Bolea et al. (2012) showed an increase in Northern Europe due to increased temperature and precipitation, while a decrease of precipitation in Southern Europe would reduce biomass accumulation. Moreover, hotter and drier conditions might replace green algae with cyanobacteria as they tolerate higher levels of desiccation (Viles and Cutler, 2012). Within Galicia (Spain), Prieto et al. (2020) did not expect a change of colonizing biomass due to climate change, decreased precipitation trends towards higher EPS production and more intense biodeterioration.

Changes in colonization were already observed in the British Isles, where the "greening" of monuments occurred due to increased algal growth (SM 6) (McCabe et al., 2011; Smith et al., 2011). The authors hypothesized that it is caused by increased wetting due to climate change and decreased levels of sulfur pollution combined and increased atmospheric nitrogen induced by vehicular pollution. Norway also expects an increase in biodeterioration and recently started a 50 years monitor program (Austigard and Mattsson, 2019). However, In Rome, biodeterioration decreased in the 20th century, attributed to a reduction in water availability after a reduction of rainfall and humidity and by increased pollution (Caneva et al., 1995). Furthermore, some biopits in Iran were no longer colonized by microorganisms. In this case, also climate conditions and air pollution were suggested as causes (Mohammadi and Krumbein, 2008). Detailed studies about the response of bacterial and archaeal communities on stones related to climate change are missing. Such research is more common in soil environments where among others, G. Li et al. (2018) and Zhang et al. (2016) detected a shift in soil bacteria after warming and altered precipitation.

8. Conclusions and future perspectives

Although there are unanswered questions about the specific impact of bacteria on building stones, extensive research has shown possible effects in the short and long term. (De Graef et al., 2005; Ettenauer et al., 2014; Gaylarde et al., 2007; Jroundi et al., 2010). On the contrary, the effects of archaea are not studied in detail. The primary question that remains unanswered is the extent to which bacteria affect their substrate compared to other microorganisms and physical or chemical deterioration. Multiple processes, such as Fe^{2+} oxidation, were successfully attributed to bacteria. Although, it is inconclusive if such processes are biologically driven within building stones. To address the explorative questions, we need an inter-and multidisciplinary approach that considers both culture-dependent and independent methodologies studying a wide spectrum of microorganisms combined with the environment and material characteristics.

Moreover, numerous bacteria successfully restored natural building stones and provided a sustainable alternative above traditional cleaning methods (Alfano et al., 2011; Romano et al., 2019; Bosch-Roig et al., 2021). Increased knowledge in bacterial and microbial communities on stones can make biological cleaning to preferred choice. Furthermore, short- and long-term surveillances should monitor the safety and effectiveness of this approach. Standardized and rapid analyses are necessary to understand the biological activity and avoid unwanted side effects (Soffritti et al., 2019).

As for now, microbial studies on monuments are often limited to a specific group of organisms, on one location using a limited number of samples. It is challenging to compare the different results as every laboratory uses a non-standardized approach and methodology. It will be beneficial to create specific databases, culture collections and to standardize the protocols among laboratories (Sterflinger et al., 2018). Standardization is challenging as methods need to be adapted for every case due to the diverse nature of the material (Piñar and Sterflinger, 2018; Sterflinger et al., 2018). Previous field studies provided valuable information about the diversity of bacteria colonizing stones and their characteristics. However, to understand their role, diversity, potential function, ecology and relationship to the environment, deeper research is necessary. One example of an extensive study is performed by Brewer and Fierer (2018), who studied 149 headstones across three continents and nine sites. They detected variations based on geographic location and climate. The communities were mainly influenced by the rock type, which also resulted in distinct functional attributes. Other parameters like headstone age, surface texture and cardinal direction of the stone face did not correlate with the microbial variation. It is important not only to identify the different taxa but also to know how the microbial populations interact with each other. In this way, it might be possible to detect the main communities and their metabolisms affecting the stone substrate positively or negatively (Perito and Cavalieri, 2018; Marvasi et al., 2019). This would allow a targeted approach to maintain or restore natural building stones. As microbial communities are not static and change along the year, more research about the seasonality of these communities, such as performed by Dyda et al. (2021), is necessary as well.

Omics-technologies have a high potential in assessing the role of bacteria and archaea on stone alteration. It contains popular methods to study microorganisms and is often preferred above traditional culture-dependent methods. Classic laboratory experiments are limited as the effect of microbial communities and a single species in its natural environment can differ significantly versus individual strains applied in the laboratory (Piñar and Sterflinger, 2018). The utility of individual strains by culture-based methods to study their potential on biodeterioration was even questioned (Gutarowska, 2020). Although, a problem with omics-technologies is the many unidentified microorganisms and chemical compounds (like metabolites) (Gutarowska, 2020). Furthermore, laboratory experiments with model organisms remain important and synthetic microbial communities should be employed on rocks as well. More standardized weathering experiments with and without naturally occurring bacterial communities or specific strains could resolve e.g. the potential role of S- and N-oxidizing bacteria on sulfuric and nitric acid formation out of air pollution. Overall, weathering experiments could help understand the biological processes and how they relate to physical and chemical alteration. Furthermore, more efforts should be done to study archaea on building stones for which optimization of the omics-technologies is necessary.

Soil research can be a good guideline for future studies on bacterial and archaeal communities of natural building stones. Soils are more extensively studied, and a lot of progress is made to understand their bacterial and archaeal communities. However, on rocks, there are still a lot of uncertainties. Within soils, they resolved e.g. the interkingdom functional diversity (Wagg et al., 2019), changes in soil bacteria after changes in weather conditions (Zhang et al., 2016; G. Li et al., 2018). Furthermore, our knowledge about the effect of EPS on rocks also mainly resolves from studies on soils (Malam Issa et al., 2009; Rossi et al., 2012b; Colica et al., 2014). These are all topics that could be investigated on rocks. It would deliver advances in our understanding within these extremely diverse environments and how they might adapt during changing climatic and other environmental conditions.

Overall, bacteria and archaea influence natural building stones, causing deterioration or protection of the substrate. While the abilities of the bacteria are well known, the precise mechanisms in the stone itself remain inconclusive. Archaea remain unexplored, and more extensive research is necessary to confirm if and which role they play. Recent progress adapting omics-technologies combined with traditional techniques will be able to unravel these complex processes. It will help our understanding of what is happening on monuments and will lead to new methods to maintain and restore our cultural heritage.

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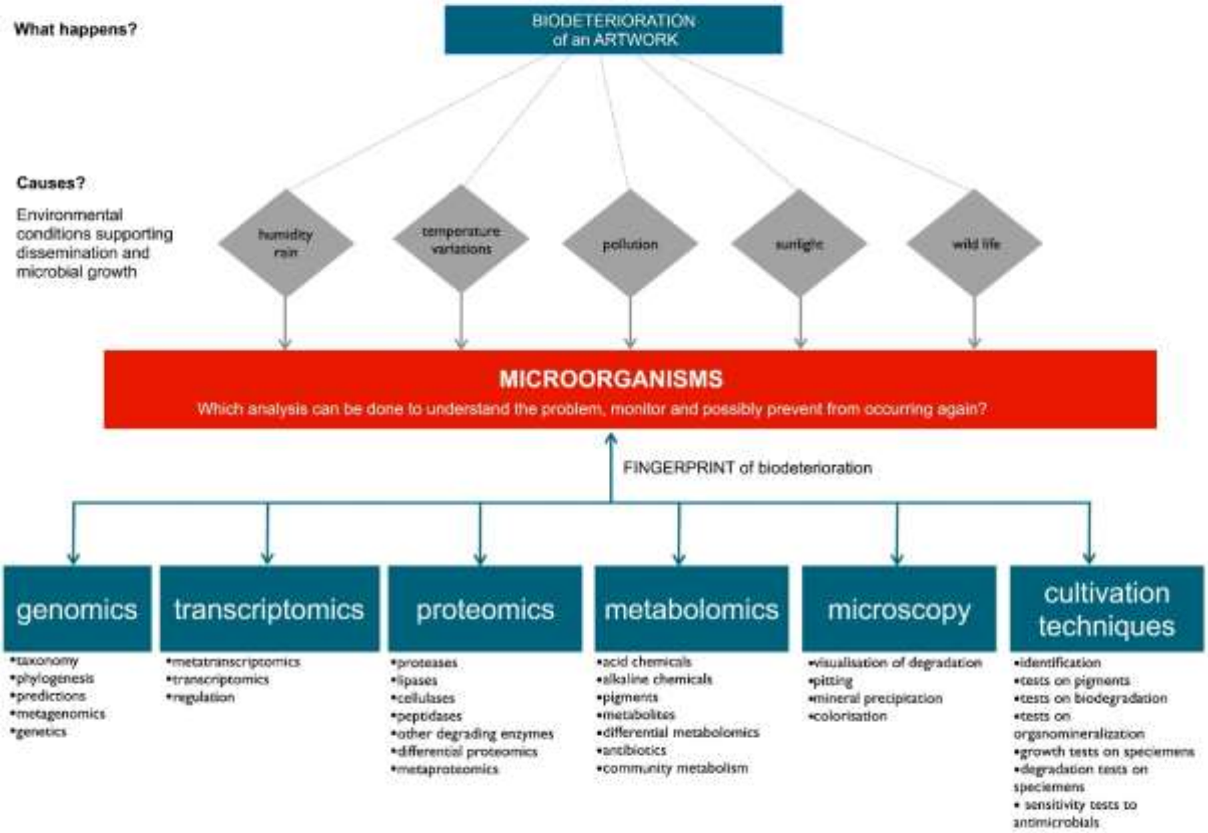

Figure 1: Flow of methods to study biodeterioration (and biocolonization in general) on cultural heritage with relation to the environmental conditions. These include the omics-technologies together with microscopy and culture-dependent techniques (Marvasi et al., 2019).