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Abstract

Microbial colonization and growth can have significant effects in the built environment, resulting in a range of effects from discolouration and staining to biodeterioration and decay. In some cases, formation of biofilms, crusts and patinas may confer bioprotection of the substrate. This perspective aims to discuss how geomicrobial transformations in the natural environment - particularly involving rocks, minerals, metals and organic matter - may be applied to understand similar processes occurring on fabricated human structures. However, the built environment may offer further strictures as well as benefits for microbial activity and these should be taken into consideration when considering analogy with natural processes, especially when linking observations of microbial biodiversity to the more obvious manifestations of microbial attack.

Introduction

Geomicrobiology is concerned with the influence of microorganisms on processes related to geology[1,2], which includes bioweathering of rocks and minerals, metal and radionuclide transformations, mineral deposition, soil formation, and biogeochemical cycling of the elements. Bioweathering is the biotic erosion and decay of rocks, stone and minerals, and is mediated through physical and biochemical mechanisms[3-6]. Biodegradation is a term applied to organic substrates that may provide a source of carbon and energy for the degrading microorganisms[7], but may be important in enhancing bioweathering by chemoorganotrophs. Biofouling results when surface microbial growth results in formation of biofilms, slimes and discolouration, but this does not necessarily result in bioweathering of the substrate[7].

As many geomicrobial processes are concerned with interactions between organisms and abiotic substrates, there can be significant consequences for human-built structures derived from rocks, minerals, and metals. In addition, the major degradative properties of microorganisms, primarily bacteria and fungi, on natural and synthetic carbon-containing materials such as wood and plastics ensure that both organic and inorganic components of human-built structures are subject to microbial influence. An understanding of geomicrobiology can assist interpretation of the colonization, biodeterioration and decay of human-built structures as well as provide information on preventative or restorative treatments. In this article, human-made structures include the built environment, nuclear repositories, industrial plant, and cultural heritage (see Box 1). The objective of this perspective is to highlight microbial roles in affecting the appearance and structure of the built environment, and to draw parallels, where possible, with geomicrobial processes occuring in the natural environment.

Sequencing-based surveys of the built environment

Biodiversity studies have shown that architectural design influences the indoor built environment microbiome[8,9] with indoor bacteria mostly comprising human-associated species and the fungal microbiome originating from outdoors[8-13]. Most studies are concerned with bacteria and human health consequences[12,14,15] rather than biodeterioration. Biodiversity studies of stone-inhabiting organisms on buildings and monuments also concentrate on bacteria[16], and few are linked with geomicrobiology. Although the number of eukaryotic studies is limited, algal and fungal communities on stone tend to exhibit low biodiversity compared to natural environments, with fungal communities being richer and heterogeneous[16]. Several taxa identified appear rare and of low ecological importance[16], while differences in the efficiency of DNA extraction methods can be extreme for microbes on building materials[17]. Although sequencing studies can provide community comparisons between sites and geographic regions[13,18], and the relative dominance of different species[18-20], there is little understanding of function or ecological interactions in a geomicrobial context[11]. Some sophisticated studies add little to earlier findings using traditional methods[11]. There are also several technological artefacts and innate biological traits that bias relative quantification of abundance[19], although a combination of electron microscopy with metabolomic and genomic techniques allowed some linkage of phylogenetic data with metabolic profiles[21]. However, such studies describe functional potential, and it is difficult to definitively link phylogeny and function[20,22]. It is clear that culture-based methods are still essential for studying geomicrobial transformations of human-made structures.

Microorganisms from all the major groups, Bacteria, Archaea and Eukarya, can operate as geomicrobial agents in a variety of contexts depending on their geoactive properties which affect organic and inorganic substrates[1-3,23,24]. This simple fact is often unappreciated in geomicrobiology where the metabolic diversity of archaea and bacteria ensures the majority of scientific attention is given to these prokaryotes to the exclusion of eukaryotes[25,26]. For example, fungi are considered to be the most important colonizers on, e.g. stone, mortar and plaster[6,27,28], and participate in many important environmental processes including elemental cycling, rock and mineral transformations, and soil formation and structure[24,29-31]. Likewise, lichens, a fungal growth form[32], are also significant biodeteriorative agents of stone monuments, buildings, cements and mortars[33-35]. Further complexity of bioweathering microbial communities arises from bacterial associations with lichens which, so far, are poorly understood[36]. Algae have major influences on global carbon cycling[37] and are ubiquitous in the built environment. Given the presence of natural materials in human-made structures, these biases are likely to carry over to studies of the built environment. This lack of attention is ironic as fungi and algae are responsible for some of the most obvious visible manifestations of microbial colonization of human-built structures.

Rock and mineral-based structures in the built environment

Bioweathering mechanisms affecting rock and mineral-based structures are identical to those in the terrestrial environment that ultimately lead to mineral soil formation[1,29,30]. In the long term, therefore, this can be considered to be the ultimate fate of rock and mineral-based human-built structures, including buildings and cultural heritage, with some added complicatory factors which may accelerate or inhibit bioweathering and biodegradation. These include climatic factors and the presence of additional structural materials, such as wood, plastic and metals, atmospheric pollution, and protective treatments.

Factors affecting microbial colonization

Stone-inhabiting microbes may grow on the surface (epilithic), in crevices and fissures (chasmolithic), or may penetrate some millimetres or even centimetres into the rock pore system (endolithic) gaining protection from environmental extremes[38]. Many organisms scavenge nutrients from the atmosphere and rainwater, and also use organic and inorganic residues on surfaces or within cracks and fissures, waste products of other microbes, decaying plants and insects, dust particles, aerosols and animal faeces as nutrient sources[27,39]. Exterior stone surfaces are usually regarded as an extreme habitat because of UV radiation, temperature and moisture variations, and lack of available nutrients[40]. Some fungal groups exhibit microcolonial or yeast-like growth forms that are effective in providing protection from heat and desiccation[23]. These may prevail under harsh conditions, and appear as black spots due to possession of UV-protective melanins[5,23,41]. Hyphae may penetrate the substratum under the colonies, while surface biomineralization may lead to the formation of robust varnish-like coatings[23,42]. Lichen cover may also offer bioprotection[5,43,44]. The accelerated deterioration that may occur if outer layers of buildings and monuments are removed for cleaning by physical and chemical methods is well documented[4,5,45]. Additionally, atmosphere-exposed microbial communities or "subaerial biofilms"[15,46] may produce protective exopolymeric substances (EPS), also capable of metal complexation, which aid colonization and survival.

The pore spaces in rocks, the endolithic environment, can also host photosynthesis-based communities that are often thought to be among the simplest ecosystems known[47]. Although this may be true in some instances, it is clear that some rock communities show considerable biodiversity[23,39,48-51]. This may be especially true of the built environment where atmospheric and anthropogenic influences may enhance colonization and growth[4,45,52] and where clear separation of endolithic and epilithic communities and their effects on the substrate are difficult to separate[28].

Microbial diversity on rock-based structures

Many rock-based structures support thriving multi-species communities that are likely to be determined by the nature of the urban environment and anthropogenic influence[39,45,52-54]. Biofilms, including cyanobacteria, green algae and fungi, are particularly evident in altering the appearance of stone structures[7,55], with fungi considered to be the most important chemoorganotrophs[56,57].

All major metabolic groups of microorganisms can be found including chemolithotrophs, chemoorganotrophs and phototrophs and biodeteriorative effects can be detected even in early stages of stone exposure[23]. Although it is usually thought that phototrophs are primary colonizers[38], it is clear that chemoorganotrophs can also be primary colonizers, achieving dominance in the absence or presence of phototrophs[4,23,58], especially where there is atmospheric organic pollution which may significantly accelerate stone decay[4,5]. Atmospheric gases, aerosols, pollutants and particulates can be accumulated in biofilms and serve as nutrient sources as well as inoculum[4,5,23]. Several bacteria and fungi can utilize organic pollutants[23] and in polluted urban environments, hydrocarbon-utilizers and sulfur-oxidizers may be enriched[59]. Organic components in the rock substrate or atmosphere also encourage chemoorganotrophic development, which in turn leads to further organic enrichment of the system through biomass production, exudation and exopolymer synthesis[4]. Which particular microbial community dominates can depend on the substrate, the atmosphere, and abiotic stresses[5,23]. Highly deteriorated stone surfaces provide appropriate conditions (a 'proto-soil') for further colonization by mosses, ferns and higher plants[6,7].

Mechanisms of rock/mineral bioweathering

The susceptibility of stone and mineral-based material to bioweathering is influenced by chemical and mineralogical composition, physical form, and geological origin[4,60,61]. The presence of weatherable minerals in stone such as feldspars and clays may provide points of weakness and significantly increase susceptibility to attack[4]**.** Typical mechanisms of microbial weathering involve physical and biochemical destruction. Physical mechanisms of bioweathering (Figure 1) include penetration by filamentous microorganisms (e.g. certain actinobacteria, cyanobacteria, algae, fungi) along points of weakness, or direct tunnelling or boring, especially in weakened or porous substrata[38,62-67]. Many cyanobacteria, not necessarily filamentous, have also been shown to have a boring ability[66]. Organisms that actively bore ("euendoliths") widely occur in cyanobacteria, red and green algae and fungi[66].

Biofilms cause weakening of the mineral lattice through wetting and drying cycles and subsequent expansion and contraction[4,23]. Lichens cause mechanical damage due to penetration of their root-like anchoring structures ("rhizines"), composed of fungal filaments, and expansion/contraction of the vegetative body ("thallus") on wetting/drying, which can lift grains of stone from the surface[68,69]. Such effects as well as thallus removal by animals, and wind, rain, hail, sleet and snow can lead to visible mechanical damage in less than 10 years[68,70]. Other physical effects on substrate integrity can be due to cell turgor pressure, and exopolysaccharide and/or secondary mineral formation[71]. The production of efflorescences ('salting') involves secondary minerals produced through reaction of anions from excreted acids with cations from the stone. Such secondary mineral formation can cause blistering, scaling, granular disintegration, and flaking or "spalling" of outer layers. This may often be a major mechanism of stone decay[5,72].

Biochemical weathering of rock and mineral substrates (Figure 1) can occur through excretion of, e.g., H^+, CO_2, organic and inorganic acids, siderophores, and other metabolites, and can occur in conjunction with biophysical mechanisms[2,71,73,74]. This can result in pitting, etching and complete dissolution. Sulfur and sulfide-oxidizing bacteria, e.g. *Acidithiobacillus* spp., are well known for their bioleaching and deteriorative actions on sulfidic-ore substrates as well as concrete, bricks and mortar[53]. Acidithiobacilli and sulfate-reducing bacteria (SRB) can be very important bacteria in biodeterioration of concrete[61]. Many bacteria, especially anaerobes, can use alternative electron acceptors for respiration, e.g. NO_3^-, SO_4^{2-}, Fe(III), and Mn(IV)[75]. The reduction (or oxidation) of such components in minerals can result in instability and dissolution[1,36]. Microbial attack on concrete appears to be mainly mediated by acidity (H^+, inorganic and organic acids) and the production of hydrophilic slimes as well as biophysical disruption[3,6,61,76,77]. In cementitious-bound concrete, the calcium oxide/hydroxide/silicate can react with CO_2 to form $CaCO_3$ ("carbonatization"). This leads to a fall in pH to around pH 8.5 which is more amenable for microbial growth. This growth in turn leads to enhanced acid production and further pH decreases to the point at which iron/steel reinforcements can become more susceptible to corrosion[3]. It is conceivable that over the long term, microbial biodeterioration of concrete and biocorrosion of metals will compromise current methods of radionuclide containment and storage.

Some organic metabolites effect dissolution by complexation of constituent metals and removal from the mineral in a mobile form. Biogenic organic acids are more effective in mineral dissolution than inorganic acids and are one of the most damaging agents affecting stone[1,4]. This underlines the importance of fungi including lichens[24,68,70,78]. Of the suite of organic acids produced by fungi, oxalate is of major significance through metal complexation and dissolution effects[78] as well as causing physical damage by formation of secondary metal oxalate biominerals expanding in pores and fissures[70,79]. Likewise, lichens produce 'lichen acids', (principally oxalic acid), which cause damage at the stone/lichen interface. Lichen thalli may accumulate 1–50% metal oxalates (the main secondary crystalline products of lichen bioweathering), depending on the substrate[34,63].

The opposing phenomenon of biomineralization, i.e. the biologically-mediated formation of minerals, is also an important component of bioweathering. This can result from, e.g. oxidation or reduction of a metal species, and metabolite excretion. Soluble Mn(II) may be oxidized by certain bacteria and fungi forming black Mn oxides, a common component of black patinas on stone[42]. Metabolites include CO_2 that can precipitate carbonates; excreted oxalate can precipitate many metal oxalates[2,24,70]. The release of metals in mobile forms from dissolution mechanisms can therefore result in various secondary mineral precipitates depending on the physico-chemical composition of the microenvironment, and these include carbonates, phosphates, sulfides and oxalates[1,2]. Such formations may contribute to physical disruption, staining and discolouration of rock and mineral surfaces, frescoes and wall paintings[41,80] (Figure 2).

Microbial biodegradation of other building materials

Brick, mortar, plaster, gypsum, grouting, glass, metals, ceramics, wood, plastic and other materials and masonry components are all subject to microbial attack[4,7,45,52,81].

Metal substrates can be subject to biocorrosion, which accounts for ~20% of all metal corrosion[5]. Most biocorrosion studies on iron, copper, and aluminium and their alloys have concentrated on pure and mixed bacterial cultures[82]. The main microbes associated with metal biocorrosion are sulfate-reducing bacteria (SRB), sulfur-, iron- and manganese-oxidizing bacteria, and general species of bacteria, algae and fungi secreting organic acids and slime, often in complex biofilm communities[82-84] (Figure 1). Mechanisms of corrosion are complicated and include depolarization of metals, biomineral formation, complexation by exopolymeric substances (EPS), H_2 embrittlement, acidic attack and electron shuttling[83] often resulting in pitting[5]. Apart from iron removal from iron and steel, SRB-mediated SO_4^{2-} reduction can lead to precipitation of FeS and blackening of metal surfaces. Bird faeces were proposed to provide a phosphate source for biotransformation of lead sheeting leading to pyromorphite formation[84]. Conversely, sulfur-oxidizers such as *Acidithiobacillus* spp. oxidize sulfur compounds generating sulfuric acid, while nitrifying bacteria produce nitric acid[3-5]; both acids attack metals, alloys and concrete, and can cause considerable damage[3]. Since alternation and stratification of aerobic and anaerobic conditions is common in natural habitats[85] and in biofilms[82,86], the processes of sulfate reduction or oxidation can occur continuously resulting in significant deterioration[83]. Microbial exopolymers and organic acids, including oxalate, are also involved in biocorrosion by metal complexation as well as acid effects[83,87]. Such biocorrosion may be enhanced by the proximity of an organic substrate, e.g. wood, acting as a reservoir of biodeteriorative microbes[87]. Fungal organic acids have been shown to corrode fuel tanks where hydrocarbon-utilizing fungi can grow at water-fuel interfaces[83].

Oxalic acid is implicated in lichen biodeterioration of asbestos roofing material, which attacks the cement matrix[88]. Lichen cover on asbestos may offer some “bioprotection” in stabilizing the surface and preventing asbestos detachment and dispersal[88,89]. Similarly, copper(II) oxalate [$Cu(C_2O_4).xH_2O$] has been found in patinas on copper metal[90]. Some of these outer formations incorporating oxalate are very stable and may also provide bioprotection from atmospheric weathering[5,43,68,91]. Biodeterioration of ceramic roof tiles by lichens has also been identified as being caused by oxalic acid excretion[92].

Glass is a ceramic material derived from silicate. All microbial groups may be involved in biodeterioration causing etching, loss of opacity and blackening, with redox transformations of, e.g. Fe, S and Mn, also causing discolouration and deterioration[5]. Medieval stained glass often shows corrosion, patina development, and mineral crust growth arising from complex microbial communities, including bacteria, fungi and lichens[93].

Biofouling, discolouration and staining

Discolouration and staining of human structures can be aesthetically unappealing and also reflect underlying bioweathering and microbial metal and mineral transformations. Such “biofouling”, often by microbial biofilms, may reflect the presence of photosynthetic pigments (cyanobacteria, algae - “greening”)[45,94] or melanins and related substances (“blackening”) produced by many surface-inhabiting fungi[4,27,95]. Biofilms may also trap dust, carbonaceous and other atmospheric particulates due to the presence of EPS[96]. These factors as well as mineralogical changes can all contribute to discolouration and the formation of patinas and crusts[4,5]. Mn(II) oxidation leads to black Mn(IV) oxide formation[42]. Rust-red or orange colours may be associated with iron oxidation[1]. Biofouling also promotes biodeterioration by shrinking or expansion and moisture retention[4].

Fungi are the principal deteriorating microbiota on painted surfaces in the built environment through colonization and biodegradation of organic components[97]. Many paint-degrading fungi are black pigmented leading to extensive discolouration of affected surfaces.

The internal environment

Outer environments clearly cannot be controlled and microbial colonization, bioweathering and biodeterioration are markedly influenced by climate and location[5]. Indoor environments are strongly influenced by human occupancy and associated activities[98], but can be controlled, particularly regarding lighting, heating, humidity and ventilation. Where these factors are not controlled, especially moisture[81], then biodegradation and biodeterioration of paper, wood, plaster and other structural components may be significant[5,81]. This is particularly important in housing where extensive internal biodeterioration by bacteria and fungi can be a health hazard[15,99], and for cultural heritage where artwork, library, museum and other collections may be permanently affected or destroyed[28,100] (Figure 1). Surface water is believed to be a prominent factor in influencing microbial changes[81]. The most important wood degraders are fungi such as various white-rot, brown-rot and soft-rot species, requiring an adequate wood moisture content to be effective[5]. Modern and ancient paper can contain large amounts of calcium carbonate[101], as well as metals arising from impurities, inks and pigments[100]. Fungal biodeterioration can result in extensive calcium oxalate precipitation[101]. Microbial activity and metal-mineral transformations in paper can also result in the formation of reddish or brown staining termed "foxing"[5]. A given indoor microbiome can also be strongly influenced by architectural design[8,9]. Further, variations in design and the use of differing building components around the world must also affect colonization and biodeteriorative effects.

Future prospects

(A) Bringing geomicrobiology into the built environment

From this brief survey, only a few main physical and biochemical mechanisms appear to be involved in microbial biodeterioration of human structures, but these are mediated by a diversity of organisms from different taxonomic and metabolic groups, and differing environmental growth requirements[1-3]. Both prokaryotes and eukaryotes are involved, and with the main exception of SRB-mediated biocorrosion, most significant organisms and processes relating to human-made structures and the built environment are aerobic, with fungi being particularly important agents of biodeterioration. This is unappreciated in many geomicrobial studies of the natural environment where the metabolic diversity of bacteria and archaea has distorted a broader view with the majority of scientific attention being given to these prokaryotes, even to the extent of solely defining them as "microbes"[26] to the exclusion of all eukaryotic microorganisms. Clearly, the presence and activities of all groups of microbes and interactions between them should be considered in any geomicrobiological studies, and this should also be the case when considering human-made structures.

In the built environment, most geomicrobial parallels should be drawn from the aerobic natural environment such as rock and mineral surfaces, and the soil "critical zone"[102], which can be defined as "that portion of the terrestrial environment characterized by a significant microbial influence on metal and mineral transformations, organic matter decomposition, and the cycling of other elements"[103]. However, a crucial difference between the natural and built environment is the significance of plant-driven bioweathering[104,105], especially the significance of mycorrhizal fungi[24]. While phototroph-driven microbial communities are significant in bioweathering in the built environment through algae, cyanobacteria and lichens, this is not always a prerequisite for bioweathering of human-made structures, or indeed in the natural environment[4,23,58]. Nevertheless, obvious analogies between built and natural environments occur regarding metal and mineral transformations and biodeterioration but often with differences in the composition of microbial communities and dominance of particular species depending on the substrate, location and climate as well as other factors. Modern DNA sequencing approaches have been applied to characterize the indoor microbiome[15], mostly concentrating on bacteria, but these techniques should also be more strenuously applied to the entire geoactive microbial communities and biofilms[46] colonizing exterior locations for better understanding of the organisms involved and their activities.

(B) Key questions that remain to be answered

It is clear that the built environment providesmany different microbially-relevant factors that affect colonization and activity compared to the natural environment. Exterior and interior components of the built environment provide a wealth of surface area, of differing compositions, textures and orientation, and all surfaces can be rapidly inoculated through atmospheric deposition and human contact[9,13]. Indoor bacterial colonization may be affected by location, e.g. room to room, ceiling versus floor, with differing bacterial communities reflecting different usage patterns rather than effects of the surface material[10,106]. There is a particular need to assess and understand the importance of substrate and design on microbial colonization and biodeterioration of interior and exterior building components to provide useful information to architects, planners, and builders. Atmospheric pollution, domestic and industrial activities, and animal exudates can further enhance deposition of potential microbial colonizers and nutrients and these processes may need to be dissected in advanced studies. While a variety of methods are available for large-scale investigations, the development of best practices, normalized methods and ideal taxonomic approaches is an ongoing problem to ensure data quality and interpretation[107]. To this end, standardized sampling and sequencing protocols may be required to obtain representative data and avoid sample processing biases, while bioinformatics approaches appear to be essential for analysing large metagenomics datasets[107].

Despite many sequencing-based and other surveys of the built environment, there are few detailed studies that combine both functional and taxonomic investigations on mineral weathering[36]. It is also difficult to separate biotic influences from purely abiotic processes[4,23,36,71,82], as is the case in natural environments. While there is little or no information on rates of bioweathering in the built environment, or on its relative significance compared to abiotic weathering, many studies on mineral bioweathering in the soil point to the importance of biotic processes in accelerating or enhancing mineral weathering above abiotic mechanisms[74,104,105]. Advances in experimental and analytical techniques, such as atomic force, advanced scanning and X-ray microscopy among others, have enabled probing of the fungus-mineral interface at a resolution necessary to allow elucidation of bioweathering mechanisms at the cellular level[67,104,108]. To extrapolate micron scale observations to the environment, experimental approaches at the macroscale are also required which can be used for modelling[104,108], although defining physico-chemical parameters in an organism-substrate interface is extremely challenging[108,109]. Experimental data combined with mathematical modelling may improve understanding of bioweathering and its significance compared to abiotic processes[108] as well as estimation of weathering rates[104,110]. Such studies suggest that the contribution of fungal-promoted mineral dissolution to biogeochemical cycling has been significantly underestimated[74,104].

Geomicrobiology is, by definition, an interdisciplinary subject area but with its own internal fragmentation, such as the prokaryotic-eukaryotic, and aerobe-anaerobe arenas, that can limit overall understanding of ecosystem functioning. In the context of the built environment, there are clear demarcations in research between bioweathering and biodeterioration studies of external surfaces and structures in the built environment, and of cultural heritage, and the microbiology of the indoor environment conducted largely in the context of human health. Most of the latter studies comprise lists of organisms and their origins, with a preponderance of bacterial attention. There is some commonality in mechanisms of bioweathering and biodeterioration with those occurring in the natural environment but, as discussed previously, there may key differences in the microbial communities involved which may be governed by the nature of the built environment under examination. Multidisciplinary and integrative studies are therefore needed to further understand bioweathering and biodeterioration, not only in the natural environment[36,111], but also those affecting human-made structures. Modern molecular techniques such as genomic sequencing can provide information on metabolic potential, estimate the significance of non-culturable organisms and relative impacts of different microbial groups, and the processes involved[36]. New bioinformatics approaches have been developed for diversity analyses and the detection of small differences between microbial communities[112]. Genes, transcripts and proteins could reveal processes and chemical intermediates that are difficult to detect by conventional geochemical approaches[113]. Despite these high-throughput approaches, and given the limitations of community and functional analysis, it is clear further endeavour is required to validate their potential. The lack of attention given to eukaryotes and mixed microbial communities, often as biofilms[46], also requires redress. Undoubtedly, standard laboratory investigations of culturable geoactive microbial species and consortia remain essential for elucidating cell physiology and the chemical, biochemical and biophysical mechanisms they employ[113].

Finally, the impact of climate change will have clear consequences for the built environment, for example through architectural design and development of low energy use buildings, shifts and migrations of human populations, and climatic effects on microbial distribution and survival. It is believed that predicted changes in climate and atmospheric chemistry, e.g. increasing temperature and atmospheric CO_2, may have a profound impact on the structure and geochemical activities of biological communities, including range shifts[114], and therefore on the organisms involved in exterior biodeterioration of the built environment and cultural heritage[115]. The biodeteriorative influence of biotic communities may therefore increase or decrease. Current modelling data suggests that vulnerable sandstone and limestone heritage structures in areas of the Mediterranean, Middle East, Caribbean and Southern Africa may be particularly affected[115].

(C) Practical significance and applications

Geomicrobial processes affecting human-made structures can have profound social and economic consequences. Some of these may be problems for the future such as the biodeterioration of nuclear repositories and waste containment systems over the long-term, and the permanent loss of cultural heritage (Figure 2). In view of the extensive new building programmes that are taking place worldwide to accommodate increasing urbanization and population growth, it is clear that geomicrobial and biodeteriorative influences should receive close attention in their design[110]. While it is impossible to prevent microbial colonization, especially of exterior locations, better understanding of the geomicrobiology of the built environment, may provide further means of prevention, control or treatment[23], or even the use of microbial systems for bioprotection. The formation of stable patinas or crusts, biofilms and lichen cover can protect the underlying substrate from further weathering, while a fungal-derived copper-oxalate patina was used for bioprotection on a copper artefact[116]. Some microbial processes may be used in biorestoration or biocleaning approaches, e.g. by removing sulfatic crusts, or degradation of glues used in frescoes[4,5]. Calcite-bioprecipitating organisms have been used for conservation of stone monuments and stone and concrete reinforcement[5].

Regarding the indoor environment, understanding of the role of the indoor microbiome in positively or negatively affecting human health has led to the concept of sustainable ”bioinformed” buildings that promote well-being, which will clearly necessitate greater communication between scientists and architects[9]. It may even be possible to incorporate design features that alter the indoor microbiome in specific locations[9]. On a broader scale, the application of integrative functional genomic methods to understand molecular dynamics and ecosystems of urban environments has implications for sustainability and future planning[107], especially with the rise of “megacities”[117]. It may be possible to create density maps of organisms relevant to the built environment, e.g. fungi, as well as determine the impact of building materials on organism distribution. Besides taxonomic and distribution information, genomic data can be mined for other purposes, such as the molecular basis of adaptation and survival[107].

Conclusions

The microbiology of human-made structures can be usefully interpreted by applying knowledge gained from geomicrobiology where there are many general parallels with the natural environment. However, the built environment does offer some particular constraints and benefits for microbial colonization, and diverse microbial communities of both pro- and eukaryotic organisms may be involved. The societal and economic consequences of microbial attack can be profound and provides a continuing interdisciplinarychallenge for researchers, builders, architects, engineers, archaeologists and historians to address. There is an urgent requirement to understand the significant roles of eukaryotes, especially fungi, interactions within mixed microbial communities, and a clear linkage between molecular-based community analysis and function. In addition to assessing the genetic and metabolic diversity of the built environment, functional and geochemical studies with individual isolates and consortia are necessary to clearly define the complex processes involved.

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G.M.G. planned and wrote the article, supplied the figures, and originated the hypotheses, ideas and conclusions therein.

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Glossary

chemolithotroph – an organism that obtains its energy from the oxidation of inorganic compounds.

chemoorganotroph – an organism that obtains its energy from the oxidation of organic compounds.

phototroph – an organism that uses light as its principal source of energy for the manufacture of organic compounds.

Box 1. The impact of biodeterioration on cultural heritage

In a societal context, a significant proportion of world cultural heritage is constructed of stone and biodeterioration can represent a permanent loss[5,6]. The most common stone types affected are marble, limestone, sandstone and granite, while materials used to stabilize building blocks (mortar) and to coat surfaces prior to painting (plaster or stucco) can also be extremely susceptible to degradation[6]. Stone cultural heritage includes buildings, paved surfaces, stone monuments, e.g. statues and gravestones), archaeological artefacts and rock art[7]. The human societal impact of geomicrobial processes on these structures includes biodeterioration, discolouration and staining, structural damage and decay, biocorrosion, altered metal mobility, and permanent disappearance. Aesthetic, cultural and economic consequences can therefore be profound (Figure 2).

Organic acids are very important bioweathering agents of cultural heritage monuments, statues, rock paintings, friezes and frescoes[4,7,63,70,78,91,118]. Calcium oxalates (whewellite and weddellite) occur widely in patinas on the surfaces of marble and limestone buildings and monuments, as well as on sandstone, granite, plasters, cave and wall paintings and sculptures[27,119-121].

Many chemoorganotrophic bacteria, archaea and fungi can colonize and deteriorate artwork including murals[5,28]. For cultural heritage, fungal growth in wall murals and frescoes can cause structural damage, and calcium and other oxalates may be produced from the calcite or metal- and mineral-containing pigments in the paint used. This can cause efflorescence, cracking, peeling and spalling of outer layers, as well as colour changes and stains[118,121]. Fungi can also degrade wood, textiles, paper, parchments, leather, glue, bone, ivory and other materials used in historical objects[28,122].

Figure 1. Some of the main influences and effects of microorganisms on components of the built environment and human-made structures. There can be many dynamic interactions between a multiplicity of physical and biochemical mechanisms in biodeterioration of rock and mineral-based substrates. Biophysical mechanisms include penetration and boring; secondary mineral formation; EPS or biomass swelling or contraction; removal of lichen thalli and adhering substratum by animals and the weather; cell turgor pressure; physical and chemical effects caused by microbial alteration of habitat geochemistry, e,g, changes in pH, redox potential, porosity, water retention, and aerobic/anaerobic transitions. Biochemical mechanisms include metabolite excretion, e.g. H^+, CO_2; organic acids, e.g. citric, oxalic; inorganic acids, e.g. sulfuric, nitric and carbonic; production of metal-complexing EPS, solvents and emulsifying agents; Fe(III)-coordinating siderophores; redox transformations by oxidation or reduction; bioaccumulation of solubilized metal and anionic species; biomineralization and formation of, e.g. carbonates, phosphates, sulfides, oxides and oxalates; alteration of habitat geochemistry by metabolism affecting metal and anionic speciation and mobility. Biodegradation of organic substances can be achieved by extracellular enzymic attack affecting many organic substrates including wood, plastics, paint, leather, paper, glues, resins, waxes, and protective coatings. Biocorrosion of metals and alloys can include sulfate reduction and metal sulfide precipitation; acid effects; redox transformations; formation of localized corrosion cells; metal complexation by exopolymers, organic acids and other metabolites; and secondary mineral formation. Scale bars on the micrographs are 50 µm.

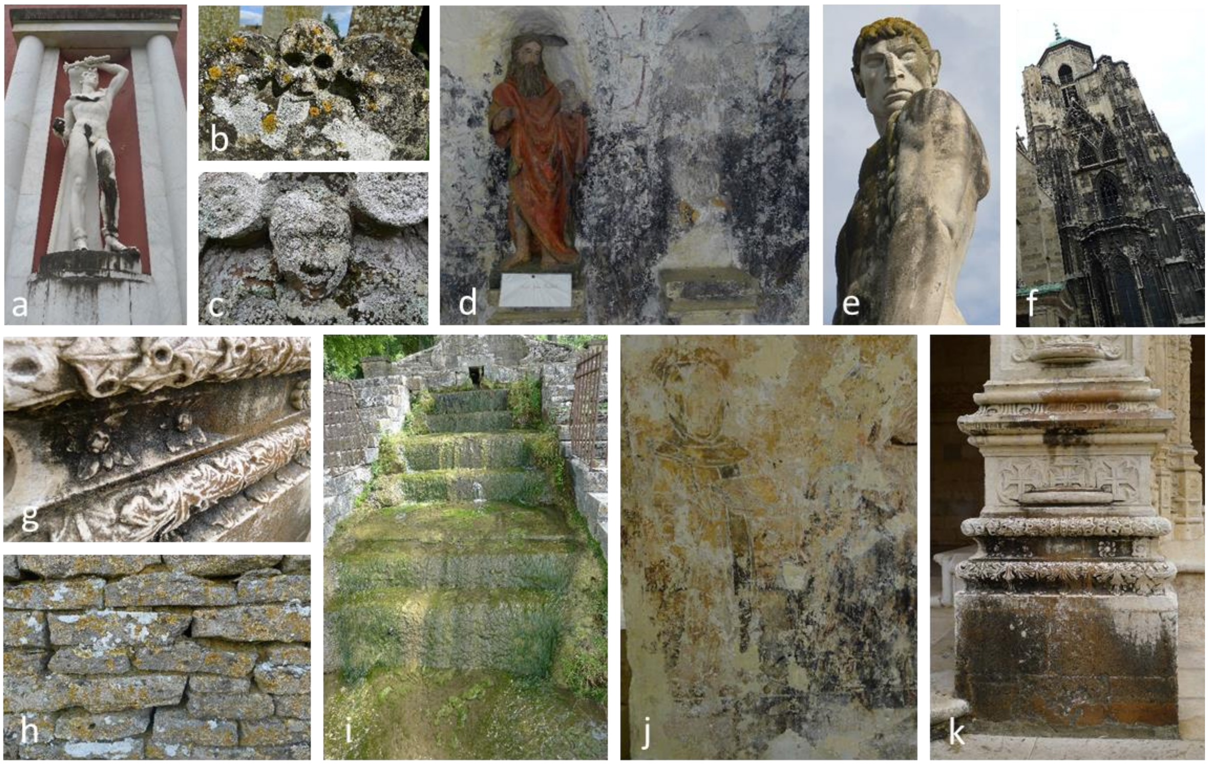

Figure 2. Examples of biofouling, discolouration, staining and biodeterioration of cultural heritage predominantly caused by algae, fungi and lichens. Greening can be the result of colonization by phototrophic microorganisms: cyanobacteria, algae and lichens. Blackening is mainly due to dark-pigmented fungi and also patina development due to various mineralogical transformations. Various colours can reflect photosynthetic or other pigments, as well as metal-mineral transformations. (a,e) historical statues (Stadio Olimpico, Rome, Italy) (b) gravestone (St Kenelm's Church, Minster Lovell, Oxfordshire) (c) gravestone (Dunbarney Burial Ground, Perth and Kinross, Scotland) (d) religious wall art and fresco (Flavigny, Burgundy, France) (f) St. Stephen's Cathedral, Vienna, Austria (g,k) monastery (Mosteiro dos Jeronimos, Belem, Portugal) (h) historic stonework (near Charlbury, Oxfordshire, England, UK) (i) ornamental fountain (Fontenay Abbey, Montbard, Burgundy, France) (j) religious wall fresco (Flavigny, Burgundy, France). Images taken by G.M. Gadd.