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Geomicrobiology of the built environment

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1 **Geomicrobiology of the built environment**

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26 Biodeterioration; Biocorrosion

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33 **Abstract**

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

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48 **Introduction**

49

50 Geomicrobiology is concerned with the influence of microorganisms on processes related to
51 geology^{1,2}, which includes bioweathering of rocks and minerals, metal and radionuclide
52 transformations, mineral deposition, soil formation, and biogeochemical cycling of the
53 elements. Bioweathering is the biotic erosion and decay of rocks, stone and minerals, and is
54 mediated through physical and biochemical mechanisms³⁻⁶. Biodegradation is a term
55 applied to organic substrates that may provide a source of carbon and energy for the
56 degrading microorganisms⁷, but may be important in enhancing bioweathering by
57 chemoorganotrophs. Biofouling results when surface microbial growth results in formation
58 of biofilms, slimes and discolouration, but this does not necessarily result in bioweathering
59 of the substrate⁷.

60

61 As many geomicrobial processes are concerned with interactions between organisms
62 and abiotic substrates, there can be significant consequences for human-built structures
63 derived from rocks, minerals, and metals. In addition, the major degradative properties of
64 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

65 human-built structures are subject to microbial influence. An understanding of
66 geomicrobiology can assist interpretation of the colonization, biodeterioration and decay of
67 human-built structures as well as provide information on preventative or restorative
68 treatments. In this article, human-made structures include the built environment, nuclear
69 repositories, industrial plant, and cultural heritage (see Box 1). The objective of this
70 perspective is to highlight microbial roles in affecting the appearance and structure of the
71 built environment, and to draw parallels, where possible, with geomicrobial processes
72 occurring in the natural environment.

73

74

75 **Sequencing-based surveys of the built environment**

76

77 Biodiversity studies have shown that architectural design influences the indoor built
78 environment microbiome^{8,9} with indoor bacteria mostly comprising human-associated
79 species and the fungal microbiome originating from outdoors⁸⁻¹³. Most studies are
80 concerned with bacteria and human health consequences^{12,14,15} rather than
81 biodeterioration. Biodiversity studies of stone-inhabiting organisms on buildings and
82 monuments also concentrate on bacteria¹⁶, and few are linked with geomicrobiology.
83 Although the number of eukaryotic studies is limited, algal and fungal communities on stone
84 tend to exhibit low biodiversity compared to natural environments, with fungal
85 communities being richer and heterogeneous¹⁶. Several taxa identified appear rare and of
86 low ecological importance¹⁶, while differences in the efficiency of DNA extraction methods
87 can be extreme for microbes on building materials¹⁷. Although sequencing studies can
88 provide community comparisons between sites and geographic regions^{13,18}, and the relative
89 dominance of different species¹⁸⁻²⁰, there is little understanding of function or ecological
90 interactions in a geomicrobial context¹¹. Some sophisticated studies add little to earlier
91 findings using traditional methods¹¹. There are also several technological artefacts and
92 innate biological traits that bias relative quantification of abundance¹⁹, although a
93 combination of electron microscopy with metabolomic and genomic techniques allowed
94 some linkage of phylogenetic data with metabolic profiles²¹. However, such studies describe
95 functional potential, and it is difficult to definitively link phylogeny and function^{20,22}. It is

96 clear that culture-based methods are still essential for studying geomicrobial
97 transformations of human-made structures.

98 Microorganisms from all the major groups, Bacteria, Archaea and Eukarya, can
99 operate as geomicrobial agents in a variety of contexts depending on their geoactive
100 properties which affect organic and inorganic substrates^{1-3,23,24}. This simple fact is often
101 unappreciated in geomicrobiology where the metabolic diversity of archaea and bacteria
102 ensures the majority of scientific attention is given to these prokaryotes to the exclusion of
103 eukaryotes^{25,26}. For example, fungi are considered to be the most important colonizers on,
104 e.g. stone, mortar and plaster^{6,27,28}, and participate in many important environmental
105 processes including elemental cycling, rock and mineral transformations, and soil formation
106 and structure^{24,29-31}. Likewise, lichens, a fungal growth form³², are also significant
107 biodeteriorative agents of stone monuments, buildings, cements and mortars³³⁻³⁵. Further
108 complexity of bioweathering microbial communities arises from bacterial associations with
109 lichens which, so far, are poorly understood³⁶. Algae have major influences on global carbon
110 cycling³⁷ and are ubiquitous in the built environment. Given the presence of natural
111 materials in human-made structures, these biases are likely to carry over to studies of the
112 built environment. This lack of attention is ironic as fungi and algae are responsible for some
113 of the most obvious visible manifestations of microbial colonization of human-built
114 structures.

115

116

117

118 **Rock and mineral-based structures in the built environment**

119

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

127

128 ***Factors affecting microbial colonization***

129

130 Stone-inhabiting microbes may grow on the surface (epilithic), in crevices and fissures
131 (chasmolithic), or may penetrate some millimetres or even centimetres into the rock pore
132 system (endolithic) gaining protection from environmental extremes³⁸. Many organisms
133 scavenge nutrients from the atmosphere and rainwater, and also use organic and inorganic
134 residues on surfaces or within cracks and fissures, waste products of other microbes,
135 decaying plants and insects, dust particles, aerosols and animal faeces as nutrient
136 sources^{27,39}. Exterior stone surfaces are usually regarded as an extreme habitat because of
137 UV radiation, temperature and moisture variations, and lack of available nutrients⁴⁰. Some
138 fungal groups exhibit microcolonial or yeast-like growth forms that are effective in providing
139 protection from heat and desiccation²³. These may prevail under harsh conditions, and
140 appear as black spots due to possession of UV-protective melanins^{5,23,41}. Hyphae may
141 penetrate the substratum under the colonies, while surface biomineralization may lead to
142 the formation of robust varnish-like coatings^{23,42}. Lichen cover may also offer
143 bioprotection^{5,43,44}. The accelerated deterioration that may occur if outer layers of buildings
144 and monuments are removed for cleaning by physical and chemical methods is well
145 documented^{4,5,45}. Additionally, atmosphere-exposed microbial communities or “subaerial
146 biofilms”^{15,46} may produce protective exopolymeric substances (EPS), also capable of metal
147 complexation, which aid colonization and survival.

148 The pore spaces in rocks, the endolithic environment, can also host photosynthesis-
149 based communities that are often thought to be among the simplest ecosystems known⁴⁷.
150 Although this may be true in some instances, it is clear that some rock communities show
151 considerable biodiversity^{23,39,48-51}. This may be especially true of the built environment
152 where atmospheric and anthropogenic influences may enhance colonization and
153 growth^{4,45,52} and where clear separation of endolithic and epilithic communities and their
154 effects on the substrate are difficult to separate²⁸.

155

156

157 ***Microbial diversity on rock-based structures***

158 Many rock-based structures support thriving multi-species communities that are
159 likely to be determined by the nature of the urban environment and anthropogenic

160 influence^{39,45,52-54}. Biofilms, including cyanobacteria, green algae and fungi, are particularly
161 evident in altering the appearance of stone structures^{7,55}, with fungi considered to be the
162 most important chemoorganotrophs^{56,57}.

163 All major metabolic groups of microorganisms can be found including
164 chemolithotrophs, chemoorganotrophs and phototrophs and biodeteriorative effects can be
165 detected even in early stages of stone exposure²³. Although it is usually thought that
166 phototrophs are primary colonizers³⁸, it is clear that chemoorganotrophs can also be
167 primary colonizers, achieving dominance in the absence or presence of phototrophs^{4,23,58},
168 especially where there is atmospheric organic pollution which may significantly accelerate
169 stone decay^{4,5}. Atmospheric gases, aerosols, pollutants and particulates can be
170 accumulated in biofilms and serve as nutrient sources as well as inoculum^{4,5,23}. Several
171 bacteria and fungi can utilize organic pollutants²³ and in polluted urban environments,
172 hydrocarbon-utilizers and sulfur-oxidizers may be enriched⁵⁹. Organic components in the
173 rock substrate or atmosphere also encourage chemoorganotrophic development, which in
174 turn leads to further organic enrichment of the system through biomass production,
175 exudation and exopolymer synthesis⁴. Which particular microbial community dominates can
176 depend on the substrate, the atmosphere, and abiotic stresses^{5,23}. Highly deteriorated stone
177 surfaces provide appropriate conditions (a 'proto-soil') for further colonization by mosses,
178 ferns and higher plants^{6,7}.

179

180

181 ***Mechanisms of rock/mineral bioweathering***

182 The susceptibility of stone and mineral-based material to bioweathering is
183 influenced by chemical and mineralogical composition, physical form, and geological
184 origin^{4,60,61}. The presence of weatherable minerals in stone such as feldspars and clays may
185 provide points of weakness and significantly increase susceptibility to attack⁴. Typical
186 mechanisms of microbial weathering involve physical and biochemical destruction. Physical
187 mechanisms of bioweathering (Figure 1) include penetration by filamentous microorganisms
188 (e.g. certain actinobacteria, cyanobacteria, algae, fungi) along points of weakness, or direct
189 tunnelling or boring, especially in weakened or porous substrata^{38,62-67}. Many cyanobacteria,
190 not necessarily filamentous, have also been shown to have a boring ability⁶⁶. Organisms that
191 actively bore ("euendoliths") widely occur in cyanobacteria, red and green algae and fungi⁶⁶.

192 Biofilms cause weakening of the mineral lattice through wetting and drying cycles and
193 subsequent expansion and contraction^{4,23}. Lichens cause mechanical damage due to
194 penetration of their root-like anchoring structures (“rhizines”), composed of fungal
195 filaments, and expansion/contraction of the vegetative body (“thallus”) on wetting/drying,
196 which can lift grains of stone from the surface^{68,69}. Such effects as well as thallus removal by
197 animals, and wind, rain, hail, sleet and snow can lead to visible mechanical damage in less
198 than 10 years^{68,70}. Other physical effects on substrate integrity can be due to cell turgor
199 pressure, and exopolysaccharide and/or secondary mineral formation⁷¹. The production of
200 efflorescences (‘salting’) involves secondary minerals produced through reaction of anions
201 from excreted acids with cations from the stone. Such secondary mineral formation can
202 cause blistering, scaling, granular disintegration, and flaking or “spalling” of outer layers.
203 This may often be a major mechanism of stone decay^{5,72}.

204 Biochemical weathering of rock and mineral substrates (Figure 1) can occur through
205 excretion of, e.g., H⁺, CO₂, organic and inorganic acids, siderophores, and other metabolites,
206 and can occur in conjunction with biophysical mechanisms^{2,71,73,74}. This can result in pitting,
207 etching and complete dissolution. Sulfur and sulfide-oxidizing bacteria, e.g. *Acidithiobacillus*
208 spp., are well known for their bioleaching and deteriorative actions on sulfidic-ore
209 substrates as well as concrete, bricks and mortar⁵³. Acidithiobacilli and sulfate-reducing
210 bacteria (SRB) can be very important bacteria in biodeterioration of concrete⁶¹. Many
211 bacteria, especially anaerobes, can use alternative electron acceptors for respiration, e.g.
212 NO₃⁻, SO₄²⁻, Fe(III), and Mn(IV)⁷⁵. The reduction (or oxidation) of such components in
213 minerals can result in instability and dissolution^{1,36}. Microbial attack on concrete appears to
214 be mainly mediated by acidity (H⁺, inorganic and organic acids) and the production of
215 hydrophilic slimes as well as biophysical disruption^{3,6,61,76,77}. In cementitious-bound
216 concrete, the calcium oxide/hydroxide/silicate can react with CO₂ to form CaCO₃
217 (“carbonatization”). This leads to a fall in pH to around pH 8.5 which is more amenable for
218 microbial growth. This growth in turn leads to enhanced acid production and further pH
219 decreases to the point at which iron/steel reinforcements can become more susceptible to
220 corrosion³. It is conceivable that over the long term, microbial biodeterioration of concrete
221 and biocorrosion of metals will compromise current methods of radionuclide containment
222 and storage.

223 Some organic metabolites effect dissolution by complexation of constituent metals
224 and removal from the mineral in a mobile form. Biogenic organic acids are more effective in
225 mineral dissolution than inorganic acids and are one of the most damaging agents affecting
226 stone^{1,4}. This underlines the importance of fungi including lichens^{24,68,70,78}. Of the suite of
227 organic acids produced by fungi, oxalate is of major significance through metal
228 complexation and dissolution effects⁷⁸ as well as causing physical damage by formation of
229 secondary metal oxalate biominerals expanding in pores and fissures^{70,79}. Likewise, lichens
230 produce 'lichen acids', (principally oxalic acid), which cause damage at the stone/lichen
231 interface. Lichen thalli may accumulate 1–50% metal oxalates (the main secondary
232 crystalline products of lichen bioweathering), depending on the substrate^{34,63}.

233 The opposing phenomenon of biomineralization, i.e. the biologically-mediated
234 formation of minerals, is also an important component of bioweathering. This can result
235 from, e.g. oxidation or reduction of a metal species, and metabolite excretion. Soluble
236 Mn(II) may be oxidized by certain bacteria and fungi forming black Mn oxides, a common
237 component of black patinas on stone⁴². Metabolites include CO₂ that can precipitate
238 carbonates; excreted oxalate can precipitate many metal oxalates^{2,24,70}. The release of
239 metals in mobile forms from dissolution mechanisms can therefore result in various
240 secondary mineral precipitates depending on the physico-chemical composition of the
241 microenvironment, and these include carbonates, phosphates, sulfides and oxalates^{1,2}. Such
242 formations may contribute to physical disruption, staining and discolouration of rock and
243 mineral surfaces, frescoes and wall paintings^{41,80} (Figure 2).

244

245

246 **Microbial biodegradation of other building materials**

247

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

250 Metal substrates can be subject to biocorrosion, which accounts for ~20% of all
251 metal corrosion⁵. Most biocorrosion studies on iron, copper, and aluminium and their alloys
252 have concentrated on pure and mixed bacterial cultures⁸². The main microbes associated
253 with metal biocorrosion are sulfate-reducing bacteria (SRB), sulfur-, iron- and manganese-
254 oxidizing bacteria, and general species of bacteria, algae and fungi secreting organic acids

255 and slime, often in complex biofilm communities⁸²⁻⁸⁴ (Figure 1). Mechanisms of corrosion
256 are complicated and include depolarization of metals, biomineral formation, complexation
257 by exopolymeric substances (EPS), H₂ embrittlement, acidic attack and electron shuttling⁸³
258 often resulting in pitting⁵. Apart from iron removal from iron and steel, SRB-mediated SO₄²⁻
259 reduction can lead to precipitation of FeS and blackening of metal surfaces. Bird faeces
260 were proposed to provide a phosphate source for biotransformation of lead sheeting
261 leading to pyromorphite formation⁸⁴. Conversely, sulfur-oxidizers such as *Acidithiobacillus*
262 spp. oxidize sulfur compounds generating sulfuric acid, while nitrifying bacteria produce
263 nitric acid³⁻⁵; both acids attack metals, alloys and concrete, and can cause considerable
264 damage³. Since alternation and stratification of aerobic and anaerobic conditions is
265 common in natural habitats⁸⁵ and in biofilms^{82,86}, the processes of sulfate reduction or
266 oxidation can occur continuously resulting in significant deterioration⁸³. Microbial
267 exopolymers and organic acids, including oxalate, are also involved in biocorrosion by metal
268 complexation as well as acid effects^{83,87}. Such biocorrosion may be enhanced by the
269 proximity of an organic substrate, e.g. wood, acting as a reservoir of biodeteriorative
270 microbes⁸⁷. Fungal organic acids have been shown to corrode fuel tanks where
271 hydrocarbon-utilizing fungi can grow at water-fuel interfaces⁸³.

272 Oxalic acid is implicated in lichen biodeterioration of asbestos roofing material,
273 which attacks the cement matrix⁸⁸. Lichen cover on asbestos may offer some
274 “bioprotection” in stabilizing the surface and preventing asbestos detachment and
275 dispersal^{88,89}. Similarly, copper(II) oxalate [Cu(C₂O₄).xH₂O] has been found in patinas on
276 copper metal⁹⁰. Some of these outer formations incorporating oxalate are very stable and
277 may also provide bioprotection from atmospheric weathering^{5,43,68,91}. Biodeterioration of
278 ceramic roof tiles by lichens has also been identified as being caused by oxalic acid
279 excretion⁹².

280 Glass is a ceramic material derived from silicate. All microbial groups may be
281 involved in biodeterioration causing etching, loss of opacity and blackening, with redox
282 transformations of, e.g. Fe, S and Mn, also causing discolouration and deterioration⁵.
283 Medieval stained glass often shows corrosion, patina development, and mineral crust
284 growth arising from complex microbial communities, including bacteria, fungi and lichens⁹³.

285

286 **Biofouling, discolouration and staining**

287

288 Discolouration and staining of human structures can be aesthetically unappealing and also
289 reflect underlying bioweathering and microbial metal and mineral transformations. Such
290 “biofouling”, often by microbial biofilms, may reflect the presence of photosynthetic
291 pigments (cyanobacteria, algae - “greening”)^{45,94} or melanins and related substances
292 (“blackening”) produced by many surface-inhabiting fungi^{4,27,95}. Biofilms may also trap dust,
293 carbonaceous and other atmospheric particulates due to the presence of EPS⁹⁶. These
294 factors as well as mineralogical changes can all contribute to discolouration and the
295 formation of patinas and crusts^{4,5}. Mn(II) oxidation leads to black Mn(IV) oxide formation⁴².
296 Rust-red or orange colours may be associated with iron oxidation¹. Biofouling also promotes
297 biodeterioration by shrinking or expansion and moisture retention⁴.

298 Fungi are the principal deteriorating microbiota on painted surfaces in the built
299 environment through colonization and biodegradation of organic components⁹⁷. Many
300 paint-degrading fungi are black pigmented leading to extensive discolouration of affected
301 surfaces.

302

303

304 **The internal environment**

305

306 Outer environments clearly cannot be controlled and microbial colonization, bioweathering
307 and biodeterioration are markedly influenced by climate and location⁵. Indoor
308 environments are strongly influenced by human occupancy and associated activities⁹⁸, but
309 can be controlled, particularly regarding lighting, heating, humidity and ventilation. Where
310 these factors are not controlled, especially moisture⁸¹, then biodegradation and
311 biodeterioration of paper, wood, plaster and other structural components may be
312 significant^{5,81}. This is particularly important in housing where extensive internal
313 biodeterioration by bacteria and fungi can be a health hazard^{15,99}, and for cultural heritage
314 where artwork, library, museum and other collections may be permanently affected or
315 destroyed^{28,100} (Figure 1). Surface water is believed to be a prominent factor in influencing
316 microbial changes⁸¹. The most important wood degraders are fungi such as various white-
317 rot, brown-rot and soft-rot species, requiring an adequate wood moisture content to be
318 effective⁵. Modern and ancient paper can contain large amounts of calcium carbonate¹⁰¹, as

319 well as metals arising from impurities, inks and pigments¹⁰⁰. Fungal biodeterioration can
320 result in extensive calcium oxalate precipitation¹⁰¹. Microbial activity and metal-mineral
321 transformations in paper can also result in the formation of reddish or brown staining
322 termed “foxing”⁵. A given indoor microbiome can also be strongly influenced by
323 architectural design^{8,9}. Further, variations in design and the use of differing building
324 components around the world must also affect colonization and biodeteriorative effects.

325

326 **Future prospects**

327

328 **(A) Bringing geomicrobiology into the built environment**

329

330 From this brief survey, only a few main physical and biochemical mechanisms appear to be
331 involved in microbial biodeterioration of human structures, but these are mediated by a
332 diversity of organisms from different taxonomic and metabolic groups, and differing
333 environmental growth requirements¹⁻³. Both prokaryotes and eukaryotes are involved, and
334 with the main exception of SRB-mediated biocorrosion, most significant organisms and
335 processes relating to human-made structures and the built environment are aerobic, with
336 fungi being particularly important agents of biodeterioration. This is unappreciated in many
337 geomicrobial studies of the natural environment where the metabolic diversity of bacteria
338 and archaea has distorted a broader view with the majority of scientific attention being
339 given to these prokaryotes, even to the extent of solely defining them as “microbes”²⁶ to the
340 exclusion of all eukaryotic microorganisms. Clearly, the presence and activities of all groups
341 of microbes and interactions between them should be considered in any geomicrobiological
342 studies, and this should also be the case when considering human-made structures.

343 In the built environment, most geomicrobial parallels should be drawn from the
344 aerobic natural environment such as rock and mineral surfaces, and the soil “critical
345 zone”¹⁰², which can be defined as “that portion of the terrestrial environment characterized
346 by a significant microbial influence on metal and mineral transformations, organic matter
347 decomposition, and the cycling of other elements”¹⁰³. However, a crucial difference
348 between the natural and built environment is the significance of plant-driven
349 bioweathering^{104,105}, especially the significance of mycorrhizal fungi²⁴. While phototroph-
350 driven microbial communities are significant in bioweathering in the built environment

351 through algae, cyanobacteria and lichens, this is not always a prerequisite for bioweathering
352 of human-made structures, or indeed in the natural environment^{4,23,58}. Nevertheless,
353 obvious analogies between built and natural environments occur regarding metal and
354 mineral transformations and biodeterioration but often with differences in the composition
355 of microbial communities and dominance of particular species depending on the substrate,
356 location and climate as well as other factors. Modern DNA sequencing approaches have
357 been applied to characterize the indoor microbiome¹⁵, mostly concentrating on bacteria,
358 but these techniques should also be more strenuously applied to the entire geoactive
359 microbial communities and biofilms⁴⁶ colonizing exterior locations for better understanding
360 of the organisms involved and their activities.

361

362 **(B) Key questions that remain to be answered**

363

364 It is clear that the built environment provides many different microbially-relevant factors
365 that affect colonization and activity compared to the natural environment. Exterior and
366 interior components of the built environment provide a wealth of surface area, of differing
367 compositions, textures and orientation, and all surfaces can be rapidly inoculated through
368 atmospheric deposition and human contact^{9,13}. Indoor bacterial colonization may be
369 affected by location, e.g. room to room, ceiling versus floor, with differing bacterial
370 communities reflecting different usage patterns rather than effects of the surface
371 material^{10,106}. There is a particular need to assess and understand the importance of
372 substrate and design on microbial colonization and biodeterioration of interior and exterior
373 building components to provide useful information to architects, planners, and builders.
374 Atmospheric pollution, domestic and industrial activities, and animal exudates can further
375 enhance deposition of potential microbial colonizers and nutrients and these processes may
376 need to be dissected in advanced studies. While a variety of methods are available for large-
377 scale investigations, the development of best practices, normalized methods and ideal
378 taxonomic approaches is an ongoing problem to ensure data quality and interpretation¹⁰⁷.
379 To this end, standardized sampling and sequencing protocols may be required to obtain
380 representative data and avoid sample processing biases, while bioinformatics approaches
381 appear to be essential for analysing large metagenomics datasets¹⁰⁷.

382 Despite many sequencing-based and other surveys of the built environment, there
383 are few detailed studies that combine both functional and taxonomic investigations on
384 mineral weathering³⁶. It is also difficult to separate biotic influences from purely abiotic
385 processes^{4,23,36,71,82}, as is the case in natural environments. While there is little or no
386 information on rates of bioweathering in the built environment, or on its relative
387 significance compared to abiotic weathering, many studies on mineral bioweathering in the
388 soil point to the importance of biotic processes in accelerating or enhancing mineral
389 weathering above abiotic mechanisms^{74,104,105}. Advances in experimental and analytical
390 techniques, such as atomic force, advanced scanning and X-ray microscopy among others,
391 have enabled probing of the fungus-mineral interface at a resolution necessary to allow
392 elucidation of bioweathering mechanisms at the cellular level^{67,104,108}. To extrapolate
393 micron scale observations to the environment, experimental approaches at the macroscale
394 are also required which can be used for modelling^{104,108}, although defining physico-chemical
395 parameters in an organism-substrate interface is extremely challenging^{108,109}. Experimental
396 data combined with mathematical modelling may improve understanding of bioweathering
397 and its significance compared to abiotic processes¹⁰⁸ as well as estimation of weathering
398 rates^{104,110}. Such studies suggest that the contribution of fungal-promoted mineral
399 dissolution to biogeochemical cycling has been significantly underestimated^{74,104}.

400 Geomicrobiology is, by definition, an interdisciplinary subject area but with its own
401 internal fragmentation, such as the prokaryotic-eukaryotic, and aerobe-anaerobe arenas,
402 that can limit overall understanding of ecosystem functioning. In the context of the built
403 environment, there are clear demarcations in research between bioweathering and
404 biodeterioration studies of external surfaces and structures in the built environment, and of
405 cultural heritage, and the microbiology of the indoor environment conducted largely in the
406 context of human health. Most of the latter studies comprise lists of organisms and their
407 origins, with a preponderance of bacterial attention. There is some commonality in
408 mechanisms of bioweathering and biodeterioration with those occurring in the natural
409 environment but, as discussed previously, there may key differences in the microbial
410 communities involved which may be governed by the nature of the built environment under
411 examination. Multidisciplinary and integrative studies are therefore needed to further
412 understand bioweathering and biodeterioration, not only in the natural environment^{36,111},
413 but also those affecting human-made structures. Modern molecular techniques such as

414 genomic sequencing can provide information on metabolic potential, estimate the
415 significance of non-culturable organisms and relative impacts of different microbial groups,
416 and the processes involved³⁶. New bioinformatics approaches have been developed for
417 diversity analyses and the detection of small differences between microbial communities¹¹².
418 Genes, transcripts and proteins could reveal processes and chemical intermediates that are
419 difficult to detect by conventional geochemical approaches¹¹³. Despite these high-
420 throughput approaches, and given the limitations of community and functional analysis, it is
421 clear further endeavour is required to validate their potential. The lack of attention given to
422 eukaryotes and mixed microbial communities, often as biofilms⁴⁶, also requires redress.
423 Undoubtedly, standard laboratory investigations of culturable geoactive microbial species
424 and consortia remain essential for elucidating cell physiology and the chemical, biochemical
425 and biophysical mechanisms they employ¹¹³.

426 Finally, the impact of climate change will have clear consequences for the built
427 environment, for example through architectural design and development of low energy use
428 buildings, shifts and migrations of human populations, and climatic effects on microbial
429 distribution and survival. It is believed that predicted changes in climate and atmospheric
430 chemistry, e.g. increasing temperature and atmospheric CO₂, may have a profound impact
431 on the structure and geochemical activities of biological communities, including range
432 shifts¹¹⁴, and therefore on the organisms involved in exterior biodeterioration of the built
433 environment and cultural heritage¹¹⁵. The biodeteriorative influence of biotic communities
434 may therefore increase or decrease. Current modelling data suggests that vulnerable
435 sandstone and limestone heritage structures in areas of the Mediterranean, Middle East,
436 Caribbean and Southern Africa may be particularly affected¹¹⁵.

437

438

439 **(C) Practical significance and applications**

440

441 Geomicrobial processes affecting human-made structures can have profound social and
442 economic consequences. Some of these may be problems for the future such as the
443 biodeterioration of nuclear repositories and waste containment systems over the long-term,
444 and the permanent loss of cultural heritage (Figure 2). In view of the extensive new building
445 programmes that are taking place worldwide to accommodate increasing urbanization and

446 population growth, it is clear that geomicrobial and biodeteriorative influences should
447 receive close attention in their design¹¹⁰. While it is impossible to prevent microbial
448 colonization, especially of exterior locations, better understanding of the geomicrobiology
449 of the built environment, may provide further means of prevention, control or treatment²³,
450 or even the use of microbial systems for bioprotection. The formation of stable patinas or
451 crusts, biofilms and lichen cover can protect the underlying substrate from further
452 weathering, while a fungal-derived copper-oxalate patina was used for bioprotection on a
453 copper artefact¹¹⁶. Some microbial processes may be used in biorestitution or biocleaning
454 approaches, e.g. by removing sulfatic crusts, or degradation of glues used in frescoes^{4,5}.
455 Calcite-bioprecipitating organisms have been used for conservation of stone monuments
456 and stone and concrete reinforcement⁵.

457 Regarding the indoor environment, understanding of the role of the indoor
458 microbiome in positively or negatively affecting human health has led to the concept of
459 sustainable "bioinformed" buildings that promote well-being, which will clearly necessitate
460 greater communication between scientists and architects⁹. It may even be possible to
461 incorporate design features that alter the indoor microbiome in specific locations⁹. On a
462 broader scale, the application of integrative functional genomic methods to understand
463 molecular dynamics and ecosystems of urban environments has implications for
464 sustainability and future planning¹⁰⁷, especially with the rise of "megacities"¹¹⁷. It may be
465 possible to create density maps of organisms relevant to the built environment, e.g. fungi,
466 as well as determine the impact of building materials on organism distribution. Besides
467 taxonomic and distribution information, genomic data can be mined for other purposes,
468 such as the molecular basis of adaptation and survival¹⁰⁷.

469

470 **Conclusions**

471

472 The microbiology of human-made structures can be usefully interpreted by applying
473 knowledge gained from geomicrobiology where there are many general parallels with the
474 natural environment. However, the built environment does offer some particular
475 constraints and benefits for microbial colonization, and diverse microbial communities of
476 both pro- and eukaryotic organisms may be involved. The societal and economic
477 consequences of microbial attack can be profound and provides a continuing

478 interdisciplinary challenge for researchers, builders, architects, engineers, archaeologists and
479 historians to address. There is an urgent requirement to understand the significant roles of
480 eukaryotes, especially fungi, interactions within mixed microbial communities, and a clear
481 linkage between molecular-based community analysis and function. In addition to assessing
482 the genetic and metabolic diversity of the built environment, functional and geochemical
483 studies with individual isolates and consortia are necessary to clearly define the complex
484 processes involved.

485

486 All correspondence to G.M. Gadd.

487

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

490

491

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501 **References**

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797

798 **Glossary**

799

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

802

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

805

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

808

809 **Box 1. The impact of biodeterioration on cultural heritage**

810

811 In a societal context, a significant proportion of world cultural heritage is constructed of
812 stone and biodeterioration can represent a permanent loss^{5,6}. The most common stone
813 types affected are marble, limestone, sandstone and granite, while materials used to
814 stabilize building blocks (mortar) and to coat surfaces prior to painting (plaster or stucco)
815 can also be extremely susceptible to degradation⁶. Stone cultural heritage includes
816 buildings, paved surfaces, stone monuments, e.g. statues and gravestones), archaeological
817 artefacts and rock art⁷. The human societal impact of geomicrobial processes on these
818 structures includes biodeterioration, discolouration and staining, structural damage and
819 decay, biocorrosion, altered metal mobility, and permanent disappearance. Aesthetic,
820 cultural and economic consequences can therefore be profound (Figure 2).

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

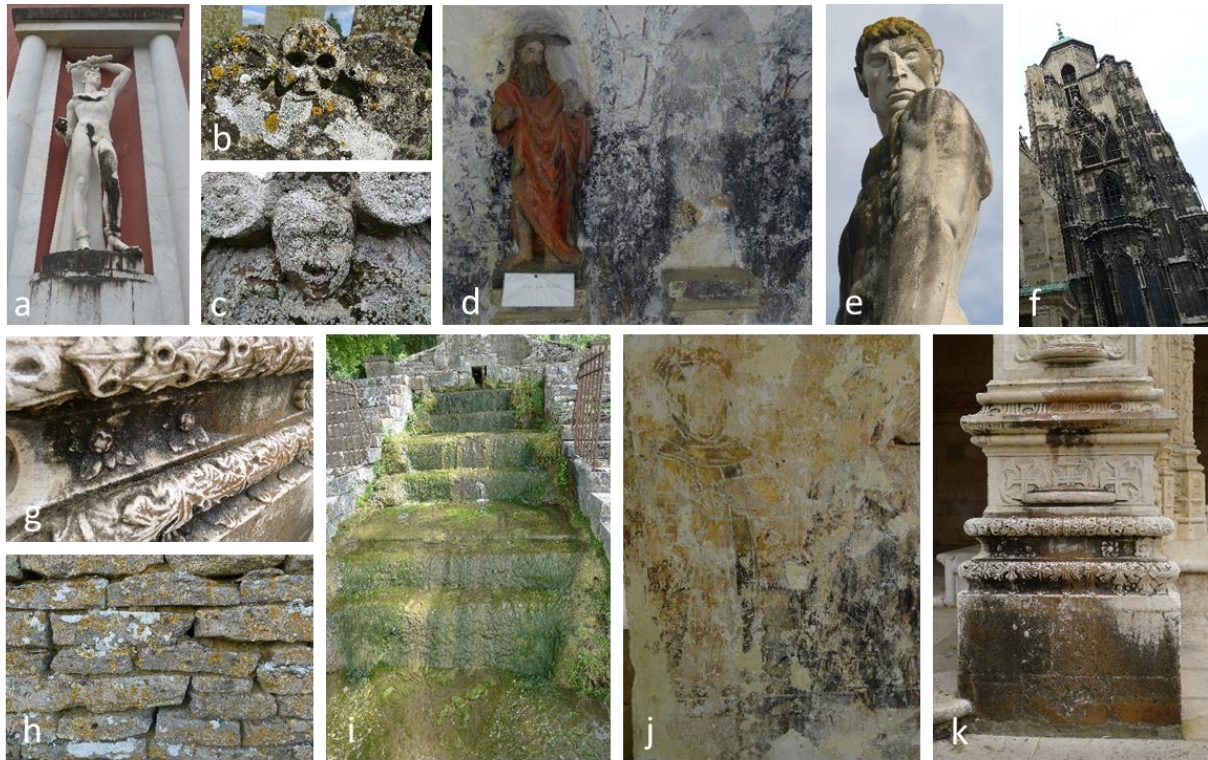
826 Many chemoorganotrophic bacteria, archaea and fungi can colonize and deteriorate
827 artwork including murals^{5,28}. For cultural heritage, fungal growth in wall murals and
828 frescoes can cause structural damage, and calcium and other oxalates may be produced
829 from the calcite or metal- and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

833

834

835 **Figure 1.** Some of the main influences and effects of microorganisms on components of the
836 built environment and human-made structures. There can be many dynamic interactions
837 between a multiplicity of physical and biochemical mechanisms in biodeterioration of rock
838 and mineral-based substrates. Biophysical mechanisms include penetration and boring;
839 secondary mineral formation; EPS or biomass swelling or contraction; removal of lichen
840 thalli and adhering substratum by animals and the weather; cell turgor pressure; physical
841 and chemical effects caused by microbial alteration of habitat geochemistry, e.g, changes in
842 pH, redox potential, porosity, water retention, and aerobic/anaerobic transitions.
843 Biochemical mechanisms include metabolite excretion, e.g. H⁺, CO₂; organic acids, e.g. citric,
844 oxalic; inorganic acids, e.g. sulfuric, nitric and carbonic; production of metal-complexing EPS,
845 solvents and emulsifying agents; Fe(III)-coordinating siderophores; redox transformations by
846 oxidation or reduction; bioaccumulation of solubilized metal and anionic species;
847 biomineralization and formation of, e.g. carbonates, phosphates, sulfides, oxides and
848 oxalates; alteration of habitat geochemistry by metabolism affecting metal and anionic
849 speciation and mobility. Biodegradation of organic substances can be achieved by
850 extracellular enzymic attack affecting many organic substrates including wood, plastics,
851 paint, leather, paper, glues, resins, waxes, and protective coatings. Biocorrosion of metals
852 and alloys can include sulfate reduction and metal sulfide precipitation; acid effects; redox
853 transformations; formation of localized corrosion cells; metal complexation by exopolymers,
854 organic acids and other metabolites; and secondary mineral formation. Scale bars on the
855 micrographs are 50 μm.

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859

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

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