REVIEW

Life in the lithosphere, kinetics and the prospects for life elsewhere

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The global contiguity of life on the Earth today is a result of the high flux of carbon and oxygen from oxygenic photosynthesis over the planetary surface and its use in aerobic respiration. Life’s ability to directly use redox couples from components of the planetary lithosphere in a pre-oxygenic photosynthetic world can be investigated by studying the distribution of organisms that use energy sources normally bound within rocks, such as iron. Microbiological data from Iceland and the deep oceans show the kinetic limitations of living directly off igneous rocks in the lithosphere. Using energy directly extracted from rocks the lithosphere will support about six orders of magnitude less productivity than the present-day Earth, and it would be highly localized. Paradoxically, the biologically extreme conditions of the interior of a planet and the inimical conditions of outer space, between which life is trapped, are the locations from which volcanism and impact events, respectively, originate. These processes facilitate the release of redox couples from the planetary lithosphere and might enable it to achieve planetary-scale productivity approximately one to two orders of magnitude lower than that produced by oxygenic photosynthesis. The significance of the detection of extra-terrestrial life is that it will allow us to test these observations elsewhere and establish an understanding of universal relationships between lithospheres and life. These data also show that the search for extra-terrestrial life must be accomplished by ‘following the kinetics’, which is different from following the water or energy.

Keywords: lithosphere; iron-oxidizing bacteria; kinetics; bacteria

1. Introduction

The detection of life on other planetary bodies would provide the opportunity to test hypotheses about the relationship between life and planetary lithospheres. It may even be possible to find common principles that govern these relationships and thus develop a coherent synthetic picture of the way in which life coevolves with planetary lithospheres throughout the Universe. To achieve this, however,

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One contribution of 17 to a Discussion Meeting Issue ‘The detection of extra-terrestrial life and the consequences for science and society’.
Figure 1. The extent of life on the Earth. Diagram depicting the thickness of the region in which there is a biota in relation to the diameter of the Earth. The thickness of the Biofilm has been increased by five times to enhance its visibility in the diagram.

requires that we first establish an understanding of the relationship between the terrestrial lithosphere and its associated life—at the time of writing our only known example of life in the Universe [1].

Despite the abundance of life on the Earth, its extent can hardly be described as a ‘biosphere’ (figure 1). In the sense that a thin-walled beach ball or a classroom geographical globe can be described as a sphere, then the term is mathematically correct. However, from a biological perspective, the biosphere is more properly termed a ‘biofilm’, which more accurately conveys the nature of the microbially dominated layer of life that covers the Earth and interacts with the lithosphere. It is consistent with the same term used to describe a layer of organisms living on or within the surface and interacting with the mineral matrices of rocks and even buildings (e.g. [2–14]). In this paper, I describe the totality of life on the Earth as the Biofilm. I have capitalized it to emphasize its application to the planetary-scale phenomenon of life. The term Biofilm also captures more exactly the phenomenon that we seek on other planetary bodies—Biofilms within the surface of planetary bodies interacting with their lithospheres and the planetary atmospheres above them.

The planetary-wide diffusion of oxygen and the distribution of carbon compounds, both produced from photosynthesis, facilitate planetary-wide heterotrophy (the use of organic carbon compounds as an energy source), and in large part account for the global contiguity and productivity of the Biofilm on the Earth today. For the present-day Earth, net productivity is estimated as approximately $1 \times 10^{16} \text{ mol C yr}^{-1}$ [15,16]. The organic acids and other metabolic products that result from this productivity contribute to the dissolution of
the lithosphere, which provides nutrients, including bioessential cations, to the Biofilm. The planetary-scale contiguity of a Biofilm is likely to be the case on any planet where oxygenic photosynthesis has evolved. This state of affairs is not my focus here.

Important questions are what productivity is achievable prior to the evolution of oxygenic photosynthesis; what kinetic barriers exist to the extraction of redox couples from the lithosphere; and what processes might facilitate the release of biologically important redox couples?

To address these questions, this paper will focus on a group of chemolithotrophs, that is, micro-organisms that use inorganic compounds as a source of electron donors for growth, called the iron-oxidizing bacteria. Iron-oxidizing bacteria are capable of using reduced iron, coupled with electron acceptors (such as oxygen in the case of aerobic iron oxidation and nitrate in the case of anaerobic iron oxidation) to conserve energy for growth. They are also capable of carrying out iron oxidation using light ([17–28]; equations (1.1)–(1.3)).

**Aerobic iron oxidation**

$$4\text{Fe}^{2+} + \text{O}_2 + 4\text{H}^+ \rightarrow 4\text{Fe}^{3+} + 2\text{H}_2\text{O}. \quad (1.1)$$

**Anaerobic iron oxidation**

$$10\text{Fe}^{2+} + 2\text{NO}_3^- + 12\text{H}^+ \rightarrow 10\text{Fe}^{3+} + \text{N}_2 + 6\text{H}_2\text{O}. \quad (1.2)$$

**Phototrophic iron oxidation**

$$4\text{FeCO}_3 + 7\text{H}_2\text{O} \rightarrow \text{CH}_2\text{O} + 4\text{Fe(OH)}_3 + 3\text{CO}_2. \quad (1.3)$$

Iron within rocks and life originates from stellar evolution as the last stable product of exothermic stellar nucleosynthesis [29]. As iron is readily incorporated at high concentrations into materials from which rocky terrestrial-type planets are formed, and it is a product of fundamental cosmological constants [30], then the use of iron as a source of electrons to drive energy acquisition in planetary lithospheres is plausibly a universal process (if life exists elsewhere). Other elements are also incorporated into rocks and can be used in energy-yielding reactions, such as sulphur, although their contribution to productivity is generally less important than iron [31]. Here attention will be given to aerobic iron oxidation. Although this reaction (equation (1.1)) requires oxygen as the terminal electron acceptor, and this would not be available (or it would be very localized) on a planet where the gross atmospheric composition remains largely unaffected by oxygenic photosynthesis, the focus here is to investigate the interactions of the organisms with the lithosphere. Thus, the choice of iron-oxidizing micro-organism does not influence the qualitative conclusions about the kinetic challenges that present themselves to the use of iron bound within planetary lithospheres.

2. Biological iron oxidation: limits of the Biofilm–lithosphere interaction

(a) Continental land environments

The first hypothesis to address is that iron within rocks provides a readily accessible source of energy for iron-oxidizing bacteria in all of the Earth’s environments.

*Phil. Trans. R. Soc. A* (2011)
Volcanic rocks (the primary igneous minerals from which the Earth is constructed, most other minerals being formed from metamorphism or sedimentary processes; [32]) usually contain between 7% and 15% iron, and most of this is available as reduced iron, either homogeneously distributed, as in volcanic glass, or localized to specific minerals, such as pyroxenes and olivines in crystalline rocks.

Studies of the microbial diversity of volcanic rocks by molecular methods yield insights into the prevalence of different groups of organisms, including iron-oxidizing bacteria. A diversity of surface volcanic rocks in Iceland have been investigated [33–37]. Analyses of the microbial diversity of these rocks (using 16S rRNA gene sequences) show that most of the organisms are related to heterotrophs. For example, in basaltic glass, *Actinobacteria* dominated the microbial community, which are a primarily heterotrophic phylum of bacteria common in soils [34].

These data are consistent with those reported by others. Gomez-Alvarez *et al.* [38] investigated microbial communities in volcanic deposits in Hawaii, USA. *Acidobacteria* and *Actinobacteria* were recovered at all sites. No sequences associated with iron-oxidizing bacteria were reported in their work. Similarly, Ibekwe *et al.* [39], in studying microbial communities associated with the ash deposits at Mount St Helens, USA, did not identify iron-oxidizing bacteria. Despite these results, in none of these studies can one rule out iron-oxidizing taxa among the large number of novel, uncultured and functionally uncharacterized organisms that are found in these environments.

The difficulty in identifying micro-organisms by molecular methods is compounded by incomplete sampling. The high number of microbial taxa in the rocks makes it difficult to achieve complete sampling of their diversity. This limitation can be partly overcome by direct attempts to culture iron-oxidizing bacteria from the rocks using gradient tube methods (e.g. [40]). Attempts to culture iron-oxidizing bacteria from many Icelandic volcanic rocks have so far been unsuccessful (P. Wilkinson 2010, unpublished data).

Neither the lack of molecular evidence for iron-oxidizing bacteria nor the lack of cultured organisms definitively shows the absence of these organisms within the rocks, but it does establish adequately the qualitative observation that the rocks are not a habitat for an abundant community of iron-oxidizing bacteria.

(b) Continental riverine environments

Two explanations for the lack of iron-oxidizing bacteria in the volcanic rocks might be a lack of these organisms generally in surficial materials in Iceland or the low temperatures experienced there. Iron-oxidizing bacteria have been described in a number of environments around the world, but most of these are deep-sea, temperate or tropical environments [41–51].

These hypotheses can be tested by searching for the presence of iron-oxidizing bacteria in potentially more favourable surface environments. Throughout Iceland small streams dissect the terrain and run through basaltic watersheds carrying the products of volcanic rock weathering. Many of them contain rocks with a conspicuous red/orange surface coloration with evident biofilms formed on their surfaces (C. S. Cockell 2009, unpublished data).
Analysis of the biofilms by scanning electron microscopy (SEM) shows them to contain abundant iron oxide spiral-shaped stalks (figure 2) and hollow iron oxide tubes associated with the iron-oxidizing genera *Gallionella* and *Leptothrix*, respectively (figure 2a–c; [52–56]). The structures are produced by the bacteria as a means to control the secretion of oxidized iron that results from iron oxidation (equation (1.1)) and prevent bacterial self-entombment [27,28,57]. Molecular analysis of the biofilms confirms the presence of 16S rRNA gene sequences belonging to *Gallionella* (figure 2d), a member of the β-proteobacteria.

Measurements of the annual temperature regimen in a typical stream ranged from 0.1 to 15.6°C during 2008. The stream did not freeze. These data support the hypothesis that abundant iron-oxidizing bacteria can persist in cold Icelandic environments and that physical environmental conditions or the lack of organisms on the island are not reasons for the lack of iron-oxidizing bacteria within the Icelandic rocks.

(c) Marine environments

The data from Icelandic streams raise the hypothesis that the presence of abundant liquid water (compared with the interior of rocks, which receives intermittent precipitation and snowmelt) is sufficient to generate a favourable environment for iron-oxidizing bacteria. This hypothesis can be further tested by examining the abundance of iron-oxidizing bacteria within basaltic rocks in the ocean environment, where the rocks are also surrounded by abundant water.

We examined young basalts (<200,000 yr) from the Axial Volcanic Ridge at an ocean depth of approximately 3 km in the median valley of the Mid-Atlantic Ridge. The basaltic glass was a composite sample of glass that had spalled off the rims of pillow basalt samples, collected by the *Isis* remotely operated vehicle (National Oceanography Centre, Southampton, UK) during cruise JC24 [58].

The samples exhibit a surface-weathered zone, which is composed of many small fractures that are filled with the alteration products of volcanic glass (figure 3) and other detritus originating from the sediments near the rocks and the photic zone. Micro-organisms inhabit the fractures and in some cases form biofilms on the fracture-filling material, which were clearly visualized in slices prepared for transmission electron microscopy (TEM; figure 3c,d).

To date, we have been unable to culture iron-oxidizing bacteria from within the rocks. Organisms we have cultured are heterotrophs associated with the ocean environments such as *Halomonas* and *Sulfitobacter* [59]. Previous studies of the microbial diversity of oceanic basalts have not revealed abundant sequences of known iron-oxidizing bacteria [60–62].

Another way to assess the presence of iron-oxidizing bacteria in this environment is to search for the depletion of iron in the basaltic glasses along fractures. If iron-oxidizing bacteria are abundant and obtaining energy from the rocks, then large iron depletions should be evident. Small samples of glass from the edge of fractures were removed by focused ion beam (FIB) milling and their elements mapped in TEM. However, there was no evidence for pervasive removal.
Figure 2. Iron oxidizers in an Icelandic stream at Skorrádalur, Western Iceland. SEM secondary electron images. (a) Image of biofilm on stream rock surfaces showing detritus mixed with frustules of diatoms and spiral stalks of the iron-oxidizing bacterium, *Gallionella* sp. (scale bar, 2 μm). (b) Close-up image of spiral stalks of iron oxides produced as waste products by *Gallionella* spp. (scale bar, 2 μm). (c) Tubes of iron oxides produced by the iron-oxidizing bacterium, *Leptothrix* sp. (scale bar, 2 μm). (d) Phylogenetic tree (16S rDNA) showing position of *Gallionella* sp. in a stream on a β-proteobacteria tree (scale bar represents number of changes per nucleotide position); *Aquifex* sp. (accession no. AB304892) was used as an outgroup. ‘River’ and ‘biofilm’ refer to two sets of sequences obtained from rock surfaces.
of iron [63]. These data are consistent with the observed association of bacteria with ferromanganese crusts on otherwise unaltered basaltic glass in the Loihi seamount, Hawaii, reported by Templeton et al. [64].

These data do not preclude an involvement of bacteria in basaltic glass alteration; indeed, considerable evidence exists that micro-organisms do interact with, and alter, basaltic glass [65–74]. However, the data provide convincing evidence that the freshly available basaltic glass does not provide a source of iron for an abundant and thriving community of chemolithotrophs.

(d) The kinetic explanation for the data

How can these three sets of data be reconciled into a synthetic view of the interactions of iron-oxidizing bacteria with the planetary lithosphere?

The contrast between the lack of iron-oxidizing bacteria in Icelandic basaltic glass and their presence in Icelandic streams can be understood as a simple kinetic problem. The basaltic glass has an iron content of approximately 13 per cent. Assuming that aerobic iron oxidation occurs with a yield whereby 0.15 moles of reduced carbon is generated from every mole of Fe$^{2+}$ oxidized [46,75] and that a bacterium contains $3.6 \times 10^{-14}$ mol C [76], then every 1 m$^3$ of basaltic glass can theoretically sustain approximately $2.5 \times 10^{16}$ iron-oxidizing bacteria. By contrast, the iron concentrations of typical Icelandic streams and rivers are sub-micromolar [77,78]. Taking an optimistic upper value of 1 $\mu$M, a stream would
sustain approximately $4 \times 10^9$ iron-oxidizing bacteria in every 1 m$^3$ of water, approximately seven orders of magnitude less biomass per unit volume than basaltic glass.

However, there are two important differences between these two environments. In the case of the basaltic glass (and all other volcanic rocks), the iron is locked up in a silicate matrix and its release rate is very low. The release rate will depend, inter alia, upon the hydrological regimen through the rocks, the presence of conditions that accelerate rock weathering, such as high or low pH, and the formation of secondary products [78–85].

Wolff-Boenisch et al. [86] calculated the release rate of major cations from igneous glasses as a function of silica content at 25°C and pH 4.0. They calculated the release rate of iron as approximately 0.003 mol m$^{-3}$ yr$^{-1}$. They assumed that the material is embedded within a soil horizon of given porosity and glass composition. This release rate would correspond to the production of $2.8 \times 10^{10}$ cells m$^{-3}$ yr$^{-1}$, if all the iron was available, or the equivalent of approximately $2.5 \times 10^4$ cells g$^{-1}$ of material. However, the low water flow rate through surface rocks in Iceland and thus near-equilibrium conditions that might exist in volcanic rock pore spaces coupled with the formation of secondary products, such as palagonite in basaltic glass [80,84], account for the lack of readily available iron to sustain iron-oxidizing bacteria over long time periods. By contrast, although per unit volume the stream has less available energy for the biota, the ferrous iron is readily accessible and is constantly replenished.

These two sets of data show how the energy in the lithosphere is generally kinetically unavailable to life, despite the thermodynamically favourable characteristics of many rocks.

A distinction should be made here between access to iron as a nutrient and access to iron as an energy supply. Some micro-organisms produce organic acids and iron-chelating compounds such as siderophores that can be used to sequester small amounts of iron from the environment for their nutrient requirements, i.e. iron for enzymes, cytochromes, etc. (e.g. [87–92]) and it is likely that these processes for deriving nutrients from the lithosphere evolved very early in the history of life [16]. However, the concentrations required for these needs are much less than those required for energy production.

It should also be observed that these data represent end-member examples and that there are environments, other than streams, where iron-oxidizing bacteria have been observed. Examples are acidic environments, where Fe$^{2+}$ is maintained in a reduced condition against oxidation in the present-day atmosphere (e.g. [93–98]), neutral wetlands [46,99] and the rock–soil interface [76].

Although the data from the Icelandic streams would suggest that the presence of water is a critical factor in enabling the kinetic limits to iron oxidation to be overcome, the mere presence of water in contact with rocks is not sufficient to release iron for energy production. The data from the Mid-Atlantic Ridge shows that voluminous water in contact with basaltic glass does not necessarily allow iron-oxidizing bacteria to derive energy from the rocks. There are two explanations for these deep-sea observations. Firstly, although iron released from the rocks might have the potential to become concentrated and useful for iron oxidation reactions, in any fractures near the surface, the iron will become diluted in ocean water within which iron is typically at

Phil. Trans. R. Soc. A (2011)
sub-nanomolar concentrations (e.g. [100,101]). Secondly, the flow of water may be insufficient to drive the surface of the rocks, particularly within enclosed fractures, far from chemical equilibrium conditions to favour further iron leaching from the rock matrix. This latter problem would also be the case for the terrestrial volcanic rocks in Iceland. These data must be reconciled with the enrichment and culture of iron-oxidizing bacteria from deep ocean basalts reported by others (e.g. [44,102–104]). Previous observations of iron-oxidizing micro-organisms in deep ocean basaltic rocks have generally been made where active circulation through rocks and hydrothermal systems generates sufficient reduced iron to sustain these communities, demonstrating the importance of an active hydrological cycle in overcoming the kinetic limitations to iron oxidation in the deep ocean.

In summary, these data illustrate the principle that the Biofilm is limited, often in many locations to the point of being unable to achieve productivity, in its ability to derive energy from the lithosphere. These limitations can only be overcome when appropriate mechanisms exist to overwhelm the kinetic barriers to the acquisition of ferrous iron from rocks. As the data presented here show, one mechanism to overcome the kinetic barrier is an active hydrological cycle, which is indirectly linked to the presence of tectonism and active volcanism. These processes can be regarded as ‘internal’ mechanisms for overcoming the kinetic barrier. An important ‘external’ mechanism is asteroid and comet impacts. To what extent can these processes overcome the kinetic barriers on a planetary scale?

3. Overcoming the kinetic barrier to lithospherically derived energy

(a) Volcanic activity and tectonism

Redox couples produced by volcanic and active geochemical and hydrological processes would have provided a diversity of energy sources on the pre-oxygenic photosynthetic Earth [31,105–107].

The primary net productivity of the present-day Biofilm has been calculated by a number of authors and is estimated to be approximately $1 \times 10^{10}$ mol C yr$^{-1}$ [15,107] with a gross productivity around twice this [107]. The potential productivity of the Biofilm without photosynthesis, and when iron is derived by a direct interaction between life and the lithosphere (i.e. direct microbe–mineral interactions), can be calculated by determining the rate of the new formation of ocean crust each year. Bach & Edwards [108] provided an estimate of the oceanic crust production of approximately $4 \times 10^9$ tonnes based on the production of approximately 3 km$^3$ yr$^{-1}$. They calculated the biomass of iron-oxidizing micro-organisms (both aerobic and anaerobic) that could be generated by this quantity of rock as approximately $1.6 \times 10^{10}$ mol C yr$^{-1}$. If the assumption of 7 per cent Fe in the rocks, as in Bach & Edwards [108], is used and the same conversion metrics as those used for the Icelandic case above are used, a total potential productivity of aerobic iron-oxidizing bacteria using iron directly extracted from the rocks would be approximately $1.5 \times 10^{12}$ mol C. Overall, the productivity of the Biofilm using Fe directly extracted from rocks would be at least six orders of magnitude less than the present-day Biofilm. This calculation assumes that all of the ferrous iron is eventually used by a biota.
Although this paper focuses on the iron-oxidizing bacteria, there are other micro-organisms that can acquire energy directly from rocks. Sulphide associated with newly formed igneous rocks can drive microbial sulphide oxidation. Bach & Edwards calculate, based on new crust formation and average sulphide concentrations, that these reactions may contribute a similar biomass as iron oxidation [108]. A variety of metal-reducing micro-organisms can use metals with multiple oxidation states to conserve energy for growth, e.g. chromium and uranium [109–111]. However, in the case of the most abundant metal available for reduction, Fe\(^{3+}\), its contribution to iron in newly formed igneous rocks is typically less than or equal to 7 per cent [112]. Although these groups of organisms will, collectively, increase the productivity of the Biofilm, the productivity of these modes of metabolism will be no greater than iron oxidation because these substrates, like iron, must be extracted from the rock matrix; in many cases these substrates are the secondary products of the oxidation of elements originally released from the lithosphere anyway.

The effects of active volcanism and geochemical cycling on productivity can be derived by calculating the productivity of a pre-oxygenic photosynthetic Biofilm \textit{in toto}, when these processes can contribute to the total productivity, a task attempted by Canfield \textit{et al.} [31]. They calculated the productivity of the Earth approximately 3.8 Ga in the absence of oxygenic photosynthesis, deriving separate estimates for productivity from H\(_2\)-based and S\(^2\)-based ecosystems and N-based ammox (anaerobic ammonium oxidation). They derived a total productivity of \(2.8 \times 10^{14} \text{mol C yr}^{-1}\). Some of the reactions considered are based on the use of atmospheric gases, e.g. nitrogen, rather than direct extraction of energy from rocks, but Canfield’s calculations give a productivity based on Fe-based anoxygenic photosynthesis of \(4 \times 10^{15} \text{mol C yr}^{-1}\), i.e. iron oxidation constitutes the majority of the total global productivity that they calculate. It should be noted that their total productivity value also includes H\(_2\)-based ecosystems, which includes H\(_2\) generated from serpentinization reactions with ultramafic rocks, which can be considered as an indirect lithospherically derived energy source. However, this energy source does not yield large productivities globally, consistent with the calculations of Sleep & Bird [106]. Canfield \textit{et al.} [31] derived their calculation of Fe-based productivity from estimates of the Archean Fe\(^{2+}\) oceanic concentration and the availability of phosphorus to support productivity. The difference between their value and the value based only on new rock production in this paper and that by Bach & Edwards [108] is probably accounted for by ocean circulation through the deep crust, and by association the tectonic and volcanic activity which contributes to active geochemical turnover and circulation in regions other than only places of new rock formation. Circulation weathers deep rocks and makes iron available which is then circulated into the oceans to allow for Fe-based ecosystems [113]. However, it should be noted that the production of new crust might have been greater on the younger hotter early Earth, which might contribute to some of the discrepancy between the biomass calculated based on new crust formation ([108]; this paper) and the estimates based on the concentration of ferrous iron in the Archean oceans [31].

Thus, in the presence of active tectonism and volcanism, which contributes to geochemical turnover and an active hydrological cycle, the productivity of the Biofilm might achieve within one or two orders of magnitude of the productivity of
the oxygenic photosynthetic Biofilm using just iron derived from the lithosphere in iron phototrophy, once the kinetic barrier to the biological use of iron has been overcome by the release of Fe\(^{2+}\) into the oceans.

\[(b)\] Asteroid and comet impact events

Asteroids and comets are the only extra-terrestrial phenomena capable of delivering a localized pulse of energy into the lithosphere. They are one of many catastrophes to which the microbial world has proven itself to be resilient over geological time periods [114]. Impact events might therefore be an important externally derived agent contributing to improving accessibility of lithospherically derived redox couples. To test this hypothesis, the effects of an asteroid or comet that has intersected with the deeper regions of the Biofilm can be investigated.

The Chesapeake Bay Impact Structure (CBIS) is a buried 85–90 km diameter impact structure formed approximately 35.4 Ma in the late Eocene [115–118]. It was formed in a shallow marine environment (water depth less than 350 m) underlain by a few hundred metres of lower Tertiary and Cretaceous sediments on top of Neoproterozoic and Paleozoic crystalline basement. The joint International Continental Scientific Drilling Programme–United States Geological Survey drilling project into the CBIS on the Eastern seaboard of the USA in 2005 offered an opportunity for the first time to investigate the influence of an impact on the Biofilm. During the drilling project, three drill cores were recovered to a depth of 1.76 km.

The recovered core reveals a sequence of events which occurred within approximately 15 minutes after the impact [119]. They include the formation of a crater cavity, the deposition of impact breccias that include suevites and air-fall deposits, the displacement of a large granite megablock from the edge of the crater overlaid by avalanching sediments and ocean-resurge (tsunami) deposits formed during the impact, and the subsequent deposition of marine sediments over the 35 Myr since impact (figure 4). We used robust contamination control to investigate the microbial communities through the impact structure [120].

The decline in microbial abundance through the top of the structure follows a logarithmic function, broadly common to, but exhibiting some important differences from, other deep subsurface sites [121]. However, from the point of view of the discussion here, the most important feature is the effect of the impact on the deeper microbial community (figure 4).

There is an increase in cell abundance below a granite megablock (below 1096 m) in a region of increased porosity, where the rocks contain fracture networks caused by the impact. Following local heating to as high as 390 °C [122], micro-organisms must have recolonized the deeper fractured region of the structure after temperatures dropped below the upper temperature limit for microbial growth at 121 °C [123]. Although we were not able to enrich iron-oxidizing bacteria, molecular methods indicated the presence of the iron-reducing genus, *Geobacter*, as members of the community. These micro-organisms perform the opposite reaction to the iron oxidizers and reduce iron with organic carbon or other electron donors. The Fe\(^{2+}\) concentrations at these depths, which exceeded 5 μmol g\(^{-1}\) sediment [124], suggest the occurrence of microbial iron reduction.

*Phil. Trans. R. Soc. A* (2011)
Figure 4. (a) Location of CBIS. (b) Microbial enumerations (log abundance per gram dry weight) through the core retrieved from the impact structure (adapted from Cockell et al. [121]). Cell numbers shown as ‘0’ are samples with cell numbers below detection limits (less than $10^4$ cells g$^{-1}$).
Although the deep regions of the impact structure did not yield iron-oxidizing bacteria, the data from the Chesapeake crater show how, by deeply fracturing rocks, impact events can enhance the flow of nutrients and redox couples through and from rocks that are otherwise inaccessible to the deeper regions of the Biofilm. Similar impacts into basaltic targets could enhance the release of ferrous iron from crustal rocks and the hydrological circulation to subsurface life.

Quantifying the effect of impacts on global productivity is difficult on account of the fact that it will depend on the scale of the impactor and it is made more uncertain by the indiscriminate target locations of impacts (unlike volcanic regions, which can be more readily constrained). Known craters on the Earth today probably cover an area of about 50,000 km² [125]. Even taking into account undiscovered craters and an impact flux 100–1000 times higher on the early Earth than today [126], the surface area directly affected by impacts at any given time on early Earth would not have been large. It would have been much less than the areas affected directly or indirectly by volcanism, tectonism and the hydrological circulation caused by these processes, particularly as higher Archean heat flow [127,128] might imply volcanism, or the influence of volcanically driven circulation, over more of the planetary surface than today. This might be different on a planet with much higher impact fluxes than those experienced on Archean Earth. Nevertheless, impacts perform an analogous process to volcanism and tectonism in the relationship between life and its lithosphere, acting to delocalize the availability of redox couples from the lithosphere, increasing planetary-scale productivity.

4. A synthetic view of the Biofilm–lithosphere interaction

On a pre-oxygenic photosynthetic planet, overcoming the kinetic barrier to the acquisition of iron as an electron donor from rocks is energetically prohibitively costly. Any process that can drive a vigorous hydrological circulation can increase the rock-weathering rate and release reduced iron from rocks, which can be coupled with electron acceptors to conserve energy for growth.

The interior of the planet, where volcanism and tectonism originates, is at too high a temperature for life. The low temperatures, desiccating conditions and high radiation levels prevent the environment of interplanetary space from hosting active micro-organisms [129], yet beneficial impactors originate from this environment. Thus, the extreme environments that define the lower and upper boundaries of the Biofilm are also the environments from which catastrophic disturbances arise that allow the Biofilm to acquire energy from the lithosphere more easily and to achieve greater planetary-scale productivity. The locations of the Biofilm’s worst threats are also the source of its enhanced productivity (summarized in figure 5).

5. The significance of extra-terrestrial life

This view of the Biofilm has implications for both the search for extra-terrestrial life and the significance of its detection.
Data show that the search for extra-terrestrial life must be guided by following the kinetics. The data from the Mid-Atlantic Ridge show that this is not the same as the strategy of following the water [130,131]. The basaltic glasses of the Mid-Atlantic Rift are surrounded by an ocean of liquid water, but the release of ferrous iron from the rocks is not sufficient to support abundant iron-oxidizing bacteria within their fractures.

Data from the Icelandic basaltic glass show that following the kinetics is not the same as the strategy of following the energy [132]. The rocks contain abundant ferrous iron in contact with atmospheric oxygen and yet the kinetic barrier makes them poor locations for iron-oxidizing bacteria.

A ‘follow the kinetics’ approach underlines the observation that habitability may not be a matter of degree, i.e. one environment is better than another or can support higher biomass. An Icelandic-like rock environment on Mars, for instance, that possessed electron donors in the form of basaltic ferrous iron, transient liquid water and electron acceptors, for example hydrogen peroxide or perchlorate in the Martian case [133,134] and a range of other required nutrients, may nevertheless be unable to support chemolithotrophic life deriving energy from crustal materials, but a river or stream may be able to do so. There can be a categorical difference between two thermodynamically favourable environments, but only one exceeds a kinetic threshold to support a particular metabolic niche.

The significance of the data for the detection of extra-terrestrial life is that an opportunity will exist to test our views of the interactions of a biota with lithospheres on another planetary body. Have other ‘life forms’ developed hitherto unimagined means for dissolving lithospheres and acquiring energy from rocks? Or is it the case that all pre-oxygenic photosynthetic planets suffer lithospheric austerity alleviated by such processes as volcanism/tectonism and impact events? Are there convergent evolutionary patterns in the mechanisms by which life extracts energy from planetary lithospheres, as is proposed for planetary megafauna [135]? What are the productivities of these other Biofilms and do these productivities follow the same quantitative trends that we observe on

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**Figure 5.** The pre-oxygenic photosynthetic Biofilm. Trapped between severe heat in the planetary interior and the freezing temperatures of outer space, it is from the former that volcanism and tectonic activity derive and from the latter that asteroids and comets originate, both of which generate the circulation to release redox couples from rocks. The Biofilm’s greatest threats are also its greatest beneficiaries.
the Earth? The detection of life on another planetary body would provide another datum point to begin to develop a catalogue, if you will, of the variations of biotic interactions with rocks, and thus to unravel universal relationships between life and lithospheres.

I would like to thank the discussion meeting organizers for the opportunity to present these data. This work was made possible by funding from the Leverhulme Trust (project no. F/00 269/N) and the Royal Society. I thank my research group for contribution of data to this paper and John Raven for valuable comments on the manuscript.

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Review. Life in the lithosphere


