Microbial Life in Impact Craters

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Abstract
Asteroid and comet impacts are known to have caused profound disruption to multicellular life, yet their influence on habitats for microorganisms, which comprise the majority of Earth's biomass, is less well understood. Of particular interest are geological changes in the target lithology at and near the point of impact that can persist for billions of years. Deep subsurface and surface-dwelling microorganisms are shown to gain advantages from impact-induced fracturing of rocks. Deleterious changes are associated with impact-induced closure of pore spaces in rocks. Superimposed on these long-term geological changes are post-impact alterations such as changes in the hydrological system in and around a crater. The close coupling between geological changes and the conditions for microorganisms yields a synthesis of the fields of microbiology and impact cratering. We use these data to discuss how craters can be used in the search for life beyond Earth.

Introduction
The collision of asteroids or comets with the surface of Earth yields large quantities of energy that cause profound changes to the geology of the target region (Melosh, 1989). The production of a fireball, blast waves,
dust-loading of the atmosphere and changes in atmospheric chemistry (Toon et al., 1997; Kring, 2003) also perturb the environment. These discoveries have focused attention on the deleterious consequences of impact events to the surface biota, focus reinforced by research on the impact thought to have been responsible for the end Mesozoic (Cretaceous–Palaeogene) extinctions (Alvarez et al., 1980; Schulte et al. 2010). Although impacts are known to have caused changes in some microbial communities; for example, the turnover in calcareous nanoplankton flora across the Cretaceous–Palaeogene boundary (Pospichel, 1996; Bown, 2005), less is known about the effects of impacts on habitats for microorganisms, particularly changes associated with geological processes. Impact events are unique among Earth-system perturbations because they are the only extraterrestrial mechanism capable of delivering a localised pulse of destructive energy into an ecosystem.

Although impacts can potentially cause global-scale environmental perturbations, asteroid and comet impacts have had a more common influence at the local scale (Kring, 1997; Adushkin and Nemchinov, 1994). An event that could cause the global changes observed at the Cretaceous–Palaeogene boundary is thought to occur at an average rate of about once per 100 million years, whereas an event causing the formation of a 1 km diameter crater with its associated environmental effects, such as those associated with the Barringer (Meteor) crater (Kring, 1997), will occur approximately once every few thousand years. Both global- and local-scale impact events will result in permanent changes to the target geology. Thus, the more common local impacts are as important in understanding how impacts alter rocky habitats for microorganisms as large events associated with global environmental perturbations.

Understanding the link between impact processes and microbiology is scientifically important from a number of perspectives. First, it gives a more complete picture of how the biosphere is shaped by geological perturbations and processes. Second, it yields insights into how the astronomical environment specifically (i.e. asteroid and comets) can shape our planet's biosphere. Third, we gain a more complete view of the role of impacts in shaping the biosphere and its subsequence evolution beyond the simplistic view that impacts 'destroy life'. Fourth, as no solar system-forming process is likely to occur without leaving behind debris, we might reasonably suggest that impact events on the surfaces of rocky planets are a universal process. Thus, understanding their influence on planetary habitability and a planetary biota provides us with a universe-scale picture of how the cosmic environment shapes the conditions for life alongside our understanding of endogenous processes within planets (such as volcanism, plate tectonics etc.) that influence planetary habitability and life.
In this paper, we review the state of knowledge on the association of microorganisms with impact craters. We highlight some of the major features of impact cratering that influence the subsequent microbial colonisation of craters. We also suggest how the study of impact-generated habitats might influence efforts to test the hypothesis of life on other planetary bodies.

**Geological changes caused by impact of relevance to microbiology**

The effects of meteorite impacts on microbiology may be defined by the sequence of geological changes that follow from such events. Meteorite impacts are characterised by an initial contact and compression stage (when the impactor makes contact with the target lithology or water), followed by an excavation phase during which a bowl-shaped "transient" crater cavity is formed; for diameters exceeding 2–4 km on Earth subsequent modification can occur, resulting in the formation of a central peak and/or peak ring, depending on the magnitude of the event (Melosh, 1989).

The kinetic energy of such an event is enormous due to the high velocity of objects intersecting with Earth's orbit (the mean impact velocity with the Earth is ~21 km/s; Stuart and Binzel, 2004). This energy will be released in large part as heat. The longevity of this thermal excursion will depend, *inter alia*, upon the target lithology, the availability of water, and local climate.

The Haughton impact structure - a 23-km diameter structure in Nunavut, Canadian High Arctic, formed about 23.5 million years ago (Young et al., 2013) - is thought to have hosted a hydrothermal system for thousands of years with initial temperatures estimated at ~650–700°C (Osinski et al., 2001; Osinski et al., 2005a), evidenced by a sequence of high temperature hydrothermal minerals such as carbonates, sulfides, and quartz followed by the precipitation of cooler temperature minerals such as sulfates. The hydrothermal system in the smaller 4-km-diameter Kärdla crater, Estonia, is also estimated to have lasted for several thousand years (Versh et al., 2005). By contrast, a lifetime of one to two million years is estimated for the hydrothermal systems of larger craters such as the 250-km-diameter Sudbury structure, Canada (Abramov and Kring, 2004) and the 170-km-diameter Chicxulub structure, Mexico (Abramov and Kring, 2007). The physicochemical environment in these hydrothermal systems will depend upon the local target lithology; however, geochemical evidence from a number of craters suggests that neutral or alkaline pH values are usual for post-impact hydrothermal systems (Naumov, 2005).

The energy delivered into the target area during contact and compression will, in addition to vaporizing the impactor, deform, heat, and metamorphose rocks (French, 2004). An important effect of shock processing is that the target rocks can become highly fractured and experience large increases in porosity. Shock-induced alteration of the
target rocks at the Vredefort (Reimold and Gibson, 1996) and Sudbury
(Ames et al., 2002) impact structures is still clearly evident today, 2.0 Ga
and 1.8 Ga after they formed, showing that these changes can persist over
geological timescales.

The formation of a crater cavity during the excavation and modification
stages will influence the local hydrological cycle through the disruption or
alteration of flow paths and also potentially through the formation of long-
lived water bodies that host aquatic microbial ecosystems. Approximately
half of the impact craters known on Earth today with clear surface
expressions host some type of intra-crater water body. Lakes formed in the
intra-crater cavity of land-based craters can persist for hundreds of millions
of years. For example, the Lac Couture impact structure in Quebec hosts a
lake approximately 430 Ma after the crater's formation; although more
recent glaciations make it unlikely that a lake has persisted for this entire
duration. However, these features are eventually subject to a breach of the
crater rim and/or infilling of the crater (this is, of course, not relevant for
impacts in the marine environment), making them, in most cases, more
short-lived than changes to the target geology.

These impact-induced geological processes influence the microbiology of
the crater and are the backdrop against which microbial communities are
re-established. Although the given sequence and duration of these impact
environments (i.e. hydrothermal system, lakes, exposed impact-altered
rocks) vary from crater to crater, they are a common theme in
understanding the distribution of microbial communities within craters.

The microbiology of impact structures
How are microbial processes linked to these geological changes
associated with impact? Data on the microbiota of impact craters is sparse
and so we examine this question by reviewing and synthesizing data from
two "type" localities - the Haughton impact structure, Canada, and the
Chesapeake impact structure, USA (Table 1). Other craters are discussed
where data are available.

Proceeding chronologically through the formation of the impact crater
environment, we propose that the first major geological effect on
microbiology is that of the shock-induced heating resulting from the transfer
of kinetic energy from the projectile to the target. The energy associated
with this process could sterilize extant microbial communities (e.g., Sleep
1989) or severely alter the ecology (e.g. Abramov and Mojzsis 2009).

Hydrothermal minerals at the Haughton structure (Osinski et al., 2001),
such as quartz, record post-impact temperatures that locally exceeded the
known upper temperature limit for microorganisms (>122°C) (Takai et al.,
2008). Similar observations have been made in the deep subsurface:
drilling of the Chesapeake impact structure has shown that at 1397 to
1424 m depth, the rock consists of 20-30% glassy impact melt clasts (Horton et al. 2009) suggesting an average temperature at the time of deposition of greater than 350°C (Malinconico et al., 2009). These data show that impact-induced sterilization can occur in surface and deep subsurface microbial communities.

As the target begins to cool, the next phase of thermally controlled microbiology can begin, where habitats for heat-loving (thermophilic and hyperthermophilic) microorganisms become available. The formation of hydrothermally-induced habitats is less well documented. Direct evidence for microbial colonisation of an impact-induced hydrothermal system is reported for the deep subsurface of the Chesapeake impact structure, where mineralised microbial structures have been observed (Glamoclija et al., 2009) and from the Siljan impact structure, Sweden where mineralized microbial biofilms associated with a low temperature hydrothermal system have been reported (Hode et al., 2009). Lipid distributions in hydrothermally precipitated gypsum in the Haughton structure have been

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**Table 1. Location, size and age of impact structures in the text of this paper***

<table>
<thead>
<tr>
<th>Name of crater</th>
<th>Country</th>
<th>Size (km)</th>
<th>Age (Myr)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Barringer</td>
<td>Arizona, USA</td>
<td>1.186</td>
<td>0.049 ± 0.003</td>
</tr>
<tr>
<td>Chesapeake</td>
<td>Virginia, USA</td>
<td>90</td>
<td>35.5 ± 0.3</td>
</tr>
<tr>
<td>Chicxulub</td>
<td>Yucatan, Mexico</td>
<td>170</td>
<td>64.98 ± 0.05</td>
</tr>
<tr>
<td>Clearwater lakes</td>
<td>Quebec, Canada</td>
<td>26 and 36</td>
<td>290 ± 20</td>
</tr>
<tr>
<td>El’gygytgyn</td>
<td>Russia</td>
<td>18</td>
<td>3.5 ± 0.5</td>
</tr>
<tr>
<td>Haughton</td>
<td>Nunavut, Canada</td>
<td>24</td>
<td>22.5 ± 2.0</td>
</tr>
<tr>
<td>Kärdla</td>
<td>Estonia</td>
<td>4</td>
<td>~455</td>
</tr>
<tr>
<td>Lonar</td>
<td>India</td>
<td>1.83</td>
<td>0.052 ± 0.006</td>
</tr>
<tr>
<td>Mjølnir</td>
<td>Norway</td>
<td>40</td>
<td>142.0 ± 2.6</td>
</tr>
<tr>
<td>New Quebec</td>
<td>Quebec, Canada</td>
<td>3.44</td>
<td>1.4 ± 0.1</td>
</tr>
<tr>
<td>Ries</td>
<td>Germany</td>
<td>24</td>
<td>14.6 ± 0.2</td>
</tr>
<tr>
<td>Rochechouart</td>
<td>France</td>
<td>23</td>
<td>203 ± 3.0</td>
</tr>
<tr>
<td>Siljan</td>
<td>Sweden</td>
<td>52</td>
<td>376.8 ± 1.7</td>
</tr>
<tr>
<td>Sudbury</td>
<td>Ontario, Canada</td>
<td>250</td>
<td>1850 ± 3</td>
</tr>
<tr>
<td>Tswaing</td>
<td>South Africa</td>
<td>1.13</td>
<td>0.22 ± 0.05</td>
</tr>
<tr>
<td>Vredefort</td>
<td>South Africa</td>
<td>300</td>
<td>2023 ± 4</td>
</tr>
</tbody>
</table>

* Data from the Earth impact database maintained by the Planetary and Space Science Centre, University of New Brunswick, Canada.
suggested to be associated with the impact hydrothermal system (Bowden and Parnell, 2007) in contrast to lipids from present-day microorganisms (Parnell et al., 2004). In Haughton specifically, the hydrothermally associated mineral assemblages are complex, including diverse mineral states of iron and sulfur. They serve as a record of geochemical conditions that varied spatially and temporally, pointing to the existence of a range of microbial habitats with different nutrient and energy availabilities, and preservation potentials (Izawa et al., 2011).

Direct evidence for post-impact colonization of a hydrothermal system might be found in isotopic signatures. Large sulfur isotope excursions in hydrothermally deposited sulfides in the Haughton impact structure are suggested to be evidence for post-impact colonization by sulfate-reducing microorganisms (Parnell et al., 2010). Similarly sulfate isotope excursions associated with impact-induced fractures are associated with the Rochechouart impact structure in France and have been hypothesized to be evidence for post-impact microbial sulfate reduction (Simpson et al., 2017).

The influence of the post-hydrothermal phase of impact cratering on biology is much better constrained, since these hydrologic systems can be observed in many craters today. The impact-induced disruption to the local geology and the formation of a crater cavity leads to the hypothesis that changes in the hydrological cycles, and therefore nutrient and redox couple supply, will influence the abundance, distribution and diversity of microbial communities. This is most clearly represented by the microbial ecosystems of intra-crater lakes. Many craters today host lakes whose microbiota have been examined; for example, the Tswaing (Ashton, 1999; Schoeman and Ashton, 1982; Ashton and Shoeman, 1983; Ashton and Schoeman, 1988), Clearwater (Maltais and Vincent, 1997), New Quebec (Bouchard, 1989; Gronlund et al., 1990), El'gygytgyn (Cremer and Wagner, 2003), and Lonar (Wani et al., 2006; Surakasi et al., 2007; Joshi et al., 2008; Antony et al., 2014) impact lakes. Microorganisms associated with impact crater lakes are also preserved in the fossil record. Fossil remains of ancient lake algal bioherms have been reported at the Ries impact structure (Riding, 1979). Few of these ecosystems are directly influenced by the fact that the cavity is impact-induced. In the case of New Quebec, the steep littoral zone that is generally a feature of crater cavities, and therefore the low biomass of peripheral photosynthesis communities, has been implicated in the low overall productivity of the lake (Gronlund et al., 1990), although a steep littoral zone is not a unique property of cavities created by impacts.

The most profound influences on a microbiota caused by an impact event, due to their potential longevity, would be expected to arise from permanent changes to the target rock, where the physical and chemical alteration of target materials by the impact would be hypothesized to change both the
availability and physicochemical characteristics of habitats for microorganisms, persisting over geological timescales.

Investigations at the Haughton impact structure, situated in what is today a polar desert (Cockell et al., 2001) have provided a particularly lucid test of this hypothesis. Evidence for the influence of impact processes on microbial colonization patterns is found in altered distributions of endolithic communities (organisms that live within the rock interstices) within shocked sandstone and gneiss lithologies (Cockell et al., 2002; Cockell et al., 2003; Pontefract et al. 2014; Pontefract et al. 2016).

Of particular interest are the shocked gneiss communities, as gneissic rocks do not generally provide suitable substrates for endolithic, especially cryptoendolithic communities, although weathering rinds can be colonized by phototrophs (chemical and biological rock weathering itself may be accelerated by impact-induced changes in the target material; Leroux, 2005; Cockell et al., 2007). The gneiss clasts within the crater, associated with the carbonate-rich melt rocks (Metzler et al., 1988; Osinski et al., 2005b; Osinski et al., 2005c), reveal an observed increase in microbial biomass and species diversity with increasing shock metamorphism (Pontefract et al., 2014, 2016); Figure 1. This is most pronounced within the photosynthetic community, where phototrophs such as Gloeocapsa and Chroococcidiopsis morphotypes are abundant within the endolithic environment, and are also found inhabiting the underside of rocks in the arctic (Cockell and Stokes, 2004; 2006). These cryptoendolithic microorganisms are limited to the interiors of rocks where pore size and permeability is sufficient to allow for the growth of the organisms throughout the rock interstices and the movement of nutrients and redox couples (Figure 2).

The cryptoendolithic colonization of gneissic rocks within the crater, specifically the enhanced colonization by phototrophs, can be explained by the effects of impact fracturing and bulking, which increased the porosity of the rocks (pore spaces of 1 micron and greater are increased in surface area by 25-fold) and the translucence of the rocks (Singleton et al. 2011). The penetration of photosynthetically active radiation through the bulk material was increased by an order of magnitude, primarily because of the formation of vesicles and fractures (Cockell et al., 2002). The organisms inhabit the upper ~5 mm of the rock substrate (Figure 1a). Although other geological events such as volcanism and earthquakes can fracture rocks, the gneissic rocks at Haughton show how impacts can cause a systemic increase in permeability, porosity and translucence throughout the rock matrix, leading to a direct cause-effect relationship between impact and the colonization of impact-shocked rocks by a specific group of microorganisms – phototrophs. This accounts for the lack of reports of cryptoendolithic communities within unweathered crystalline rocks in other geological settings. The community composition between low shock and
high shock is also different in non-phototrophic taxa (Pontefract et al. 2016).

Detailed examination of shock gneisses, whereby shock levels were estimated from petrographic analysis and correlated to microbial colonisation allowed for the quantification of the optimal shock range in which the habitat is improved for colonisation. This was found to be between 55 and 65 GPa (Pontefract et al., 2014). This study examined the depth distribution of organisms into shocked gneisses and using confocal

Figure 1. Cryptoendoliths associated with impact-altered rocks. Location of organisms is indicated with arrows. a) Cryptoendolithic phototrophs associated with impact-altered gneiss (shocked to ~30 GPa) from the Haughton impact structure, Nunavut, Canadian High Arctic, b) similar communities associated with vesiculated and shocked sandstones (~10-20 GPa) from the same impact structure. Scale bar 1 cm.
Microscopy the direct link between the fractures, pore spaces, and microbial colonisation was demonstrated.

Microbial diversity within impact-shocked rocks is also correlated with shock metamorphism. In the Haughton impact structure, species diversity was found to increase in gneisses exposed to higher shock pressures (Pontefract et al., 2016), with distinct populations based on the level of porosity and light transmission within the rock. In each population of organisms studied, Actinobacteria were the most abundant phylum, and it was not until shock pressures of 55 GPa were attained that phototrophic...
bacteria began to represent a significant portion (>10%) of the microbial community. The study found that these effects on microbial diversity are likely caused by a variety of influences resulting from the impact processing of the gneissess, such as changes in surface area available for growth and changes in fluid flow and nutrient availability, and potentially the effects of changed primary production from the greater abundance of phototrophs observed at higher shock levels. The study demonstrates that impact events can change the microbial diversity that can be supported by the target location.

Although the shocked rocks at Haughton are chemically varied (Metzler et al., 1988), it was possible to examine the effects of impact shock on major and trace elements. Pontefract et al. (2012) showed that major cation abundances expressed as oxides were lower in highly shocked crystalline rocks compared to lower shocked rocks. Concentrations peaked at shock level 3 (~10-30 GPa), which could be an artefact of the fact that unshocked or very low-shocked rocks sourced outside the crater do not exactly match the pre-impact basement below the crater. These patterns were not observed for trace elements, which could be explained by these elements being associated with more stable phases within the rock. Similar patterns were not observed in sedimentary rocks. In some cases, the concentration of some elements such as phosphorus increased, which they attributed to possible hydrothermal mobilisation of phosphorus or enrichment by organisms on account of enhanced colonisation. The authors note that the formation of glasses by high shock pressures may enhance element availability to a biota since glasses are more easily dissolved by organic acids than crystalline rocks. Thus, the physical changes in the rock may change elemental availability.

The formation of glasses by impact events may offer entirely new habitats for life. Tubular structures in volcanic glasses have long been associated with microbial boring (e.g., Staudigel et al., 1995, 1998; Torsvik et al., 1998; Thorseth et al., 1991) although specific occurrences remain controversial and the means of their formation remains a matter of discussion. Tubular features have been observed in impact glass–bearing breccias from the Ries impact structure (Sapers et al., 2014). These features have associated with them organic features observed using Fourier transform infrared (FTIR) spectroscopy. These features raise the possibility that impact glasses may provide habitats for microorganisms capable of active boring. Furthermore, if they are biogenic, they demonstrate potential as biosignatures of life in preserved impact glasses.

Though the impact-induced changes in rocky microbial habitats discussed above have been shown to have a linear correlation (though a more complex model may be supported by the data) with increasing shock metamorphism (Pontefract et al. 2014), not all rock types conform to this type of relationship. Investigations on the effects of shock on the
colonization of sandstones within the Haughton impact structure reveal complexities in the correlation between shock level and colonization associated with the rock type (Osinski, 2008; Cockell and Osinski, 2007) (Figure 1b, 3 and 4). As the sandstones are exposed in the same locations and experience the same environmental conditions as the shocked gneisses, they offer a comparison to the crystalline rocks. Whereas unshocked sandstones are generally porous and suitable for endolithic colonization (Friedmann, 1982; Wessels and Büdel, 1995; Weber et al., 1996; Colwell et al., 1997; Büdel et al., 2004; Blackhurst et al., 2005; Omelon et al., 2006), crystalline rocks are not. A comparison between the two lithologies yields insights into effects of impact on rocky microbial habitats with quite different initial conditions for microbial colonization.

At low shock pressures (<5.5 GPa), sandstones were found to suffer from pore collapse (Osinski, 2008), which impeded colonization by a laboratory-cultivated cyanobacterium *Chroococcidiopsis* sp. and the Gram-positive bacterium *Bacillus subtilis*, consistent with expectations from previous geological observations of shocked sandstones (Kieffer, 1971; Kieffer et al., 1976; Osinski, 2008). However, at higher shock pressures, the formation of

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**Figure 3.** Schematic diagram illustrating the potential for colonization of sandstones with respect to shock level. 'Colonisation potential' means the accessibility of the rock interior for colonisation. This general schema can be modified to any type of material, but illustrates some of the complexities that influence colonisation potential. Low shock (class 1b; ~3-5.5 GPa, porosity ~2-5%) was found to close pore spaces and retarded colonisation. Beyond these shock pressures and up to ~20-30 GPa (up to class 5; 30-36% porosity), production of vesicles in the glass improved permeability and colonisation, although recrystallization in some samples was noted to reduce accessibility to organisms. At shock pressures greater than ~35GPa (class 6), recrystallization was observed to an extent that microorganisms could no longer colonise these materials (taken from Cockell and Osinski, 2007).
vesicles in the rock, caused by irregular patterns of melting, improved colonization. Natural cyanobacterial colonization of sandstones shocked to 10-20 GPa is observed in field samples (Figure 1b). At yet higher shock pressures (~35 GPa) cryptoendolithic colonization may again be impeded by recrystallization and the formation of solid glassy material. Although a systematic pattern can be discerned as illustrated in Figure 3, shock processes are heterogeneous, even at centimeter scales, leading to irregular colonization patterns depending on where the shock wave has generated compressed pores, glass and/or vesicles (Figure 4d). The data show that impacts cause quite specific increases or decreases in colonization potential that are linked to specific shock levels.

In summary, impacts can, in the same target location, cause geomicrobiological conditions to be reversed. Low porosity crystalline rocks that are typically difficult for microorganisms to colonize can be improved as habitats due to fracturing and vesicularisation. By contrast, high porosity rocks, such as sandstones, can, at certain shock pressures, be impoverished with respect to their accessibility to a biota.

Impact events can generate new habitats by mobilising fluids that precipitate new minerals, for example in hydrothermal systems. In the Haughton impact structure, the colonization of hydrothermally deposited calcium sulfate (selenite) was demonstrated, whereby microorganisms colonise the cleavage planes in selenite (Parnell et al., 2004). As the material is transparent to photosynthetically active radiation, the spaces can act as habitats for phototrophs.

Across a wide range of rock types, impact events fracture materials, generating new habitats for chasmoendoliths that inhabit the fractures connected to the surface of rocks. These effects are less subtle than the changes in internal permeability described above for gneiss and sandstone and relate more to the general shattering of target rocks. The fracturing of carbonates is observed in Haughton that provide habitats for a diversity of
microorganisms, for example in ejecta blocks (Cockell et al., 2003). Fractures are also produced in exposed outcrops of gypsum that harbor a diversity of phototrophs and heterotrophs (Cockell et al. 2010).

In addition to the physical effects of shock metamorphism, the thermal effects on any indigenous organic carbon in the crater is a constraint. This carbon contributes to what is available for reprocessing as biomass by subsequent colonisers. However, the carbon becomes more thermally mature due to the energy of impact, as measured in the Haughton Crater (Parnell et al. 2005, Lindgren et al. 2009), and less amenable to reprocessing.

A large quantity of the diversity and biomass of microbial life on the Earth resides in the subsurface (Whitman et al. 1998; Horsfield et al., 2007; Kallmeyer et al., 2012; Magnabosco et al., 2018). The drilling of the Chesapeake Bay impact structure (Gohn et al., 2008) using microbiological contamination control (Gronstal et al., 2009) allowed the changes in the deep subsurface caused by impact events to be examined (Cockell et al., 2009). The crater was formed in the Late Eocene and is approximately 35 million years old (Koeberl et al. 1996; Powars and Bruce, 1999; Poag et al., 2004; Hortson et al., 2005). The buried structure has the form of an inverted sombrero and a 1.6 km core was collected within the elliptical moat approximately 9 km from its centre (Gohn et al., 2008). The microbiology of the crater core (Figure 5) can be broadly split into three zones (Cockell et al., 2009). The upper zone (127-867 m depth) exhibits a logarithmic decline in cell numbers similar to other deep subsurface environments, with cell numbers declining to below detection limits within the middle parts of the tsunami resurge deposits that filled the crater cavity following the impact. The steeper decline in cell numbers with depth associated with this zone compared to the rate of reduction in cell numbers with depth in other subsurface sites (Parkes et al., 1994; D'Hondt et al., 2004) may be a general feature of the terrestrial biosphere. Alternatively, it may be specifically linked to a change in geochemical conditions, such as the increasing salinity of the water within the crater with depth, which is a result of the inundation by seawater at the time of impact along with the redistribution of a subsurface brine layer thought to be pre-impact in origin (Sanford, 2003; Sanford et al., 2009).

A second zone within the crater (867-1397 m depth) exhibits cell counts below detection limits, sections where cells were not cultivatable and DNA could not be recovered. The hydrological data suggest that neither the introduced seawater nor the pre-impact briny water within the section has been flushed since impact. This interval may have remained biologically impoverished since impact.

More direct evidence for an impact-induced effect on the habitat for microorganisms was found in the third microbiological zone in the crater
Figure 5. Enumeration of microorganisms with depth through the Chesapeake Bay impact structure. The lithological sequence through the post-impact sediments and the crater is shown on the left. Enumerations (right) can be split into three distinct zones. Zone 1 is a region with a logarithmic decline in the post-impact sediments and the upper part of the impact tsunami deposits. Zone 2 is a region with enumerations below detection limits and Zone 3 is a region of fractured rock below a granite megablock. The detection limit of enumerations was taken as $10^4$ cells/g.
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(below 1397 m depth) associated with a rise in microbial abundance beneath a granite block that slumped into the crater cavity in the final stages of the impact event. The lower part of this zone is associated with fractured schist-pegmatite rock. Impact breccia veins and dykes that contain shock-deformed rocks are locally present, often associated with fracture networks.

Although we do not have enumeration data for unaltered material immediately outside the crater at a corresponding depth, cell abundances three orders of magnitude lower were observed in samples collected from cores taken northwest of the crater rim in the Coastal Plain (Chapelle et al., 1987). The layered sections in this core represent the geologic units of the original target material and provide the only comparison of unaltered material. These data suggest that the impact and post-impact processes contributed to an increase in the porosity of this region of the crater and played a role in the formation of fracture networks through which microorganisms could have migrated. The presence of breccia dykes within the material suggests that dilatancy, or the opening of fractures, occurred during their emplacement, which would have contributed to biological recolonization. In addition, compaction of crater fill material over time resulted in an upward advection of fluids that may have enhanced microbial recolonization.

The data obtained from the deep subsurface of the Chesapeake structure show that impacts can change the conditions for microbial communities for many millions of years after the event. The deep melt-rich sections of the crater provide evidence that the shock wave and its associated thermal excursion sterilized the deep subsurface, but the fracture networks and advection later allowed recolonization and movement of both redox couples and nutrients into the units of the crater cavity, improving the environment for life.

The data from the Haughton and Chesapeake impact structures, when considered together, show that despite general observable changes in geology caused by impact, particularly rock fracturing (Gurov and Gurova, 1983; Henkel, 1992; Pilkington and Grieve, 1992; Pesonen et al., 1999; Plado et al., 2000; Salminen, 2004; Kumar, 2005; Kumar and Kring, 2008) whose biological effects were noted in earlier work (Cockell and Lee, 2002; Cockell et al., 2005), the particular geological effects of asteroid and comet impacts allow us to discriminate their influence on habitats for microbial communities compared to other geological agents that fracture or compress rocks.

Successional changes in the biota

The changes described above can be presented within the context of classical ideas of ecological succession, which allows for the suggestion of some major successional phases associated with impact craters. A first
phase, a phase of thermal biology, is associated with the hydrothermal systems established in the impact crater and around it (Cockell and Lee, 2002). It will last for as long as the hydrothermal systems persist. In some cases, where the heating is insufficient, for example in small impacts, the influence of the heating on the local biota will be inconsequential. These systems are analogous in some ways to colonisation of deep-sea hydrothermal vents (Sylvan et al., 2012; Christakis et al., 2017; Patwardhan et al., 2018). However, impact systems would be different in two major respects. First, impacts can occur indiscriminately in any lithology. Thus, the geochemistry of the fluids generated, and the subsequent conditions for life, will depend uniquely on the flow regime and geology of the target site. Of course, impact can occur into land, which will greatly differ in terms of fluid circulation and the cooling and diluting influences of the ocean in the case of hydrothermal vents. Second, the temperature regimes in impact craters will depend on the scale of the impact and the distribution of heat, which itself will depend on the target lithology. In general, unlike hydrothermal vents, which are localised point sources of heat, impact events are distributed sources of heat which gradually cool. The rate of cooling will again depend on the target material and the initial distribution of heat during impact. After cooling, or in regions unaffected by the hydrothermal system, colonization will occur by non-thermophilic organisms. This successional transition has clearly occurred in the shocked rocks of the Haughton impact structure in the present-day.

The subsequent changes that occur in the crater amount to a long-term phase of post-impact succession and climax in which microbial ecosystems become established that correspond to the gross geological changes occurring in and around the crater. For example, the formation of the crater cavity can lead to the formation of an intra-crater lake as observed in many craters today, with their associated biota (Ashton, 1999; Schoeman and Ashton, 1982; Ashton and Shoeman, 1983; Ashton and Schoeman, 1988; Bouchard, 1989; Gronlund et al., 1990; Malais and Vincent, 1997; Cremer and Wagner, 2003; Wani et al., 2006; Surakasi et al., 2007; Joshi et al., 2008; Antony et al., 2014). There may later be a phase of colonization of intra-crater lake sediments if the crater rim is breached and a lake is drained (Hickey et al., 1988). Successional changes will occur as new organisms are blown into the crater and colonise the various available substrates. In the case of impact events in aquatic habitats, successional changes will be associated first with local disruption of the overlying water column, and possibly sediments, such as seems to have been the case at Mjølnir, Norway (Smelror and Dypvik, 2006). These lake successional events are not unique to impact craters *per se*, but the crater cavity, the confining effects of the rim, the potential for the residual influence of the hydrothermal system *etc.* underscore the fact that the geological and thermal changes caused by a given impact will influence the nature of successional changes and the biota that occur in that location.
Shocked lithologies will change the habitats for microorganisms, as has already been reviewed, throughout all of these phases. The communities that colonize impact-metamorphosed rocks observed in craters today are, in most cases, unlikely to be the same as the communities that did so immediately after the impact. There is no new crater existing today in which immediate post-successional microbial communities can be examined. The communities either taking advantage of shocked rocks, or excluded from deleteriously altered lithologies, will be influenced by the regional climate in which the impact occurs, and in the early stages after impact, possibly the impact hydrothermal system and intra-crater water bodies. However, in the case of the rocks at Haughton, for instance, the bulk chemistry and physical features of the rock have not been substantially altered by non-impact processes. Therefore, the colonization of the rocks and the effects of impact on them can be considered to provide a faithful insight into the effects of impact on microbial recolonization processes.

A late phase of ecological assimilation in which erosion of the crater causes the ecology to become indistinguishable from the outlying ecology was suggested (Cockell and Lee, 2002). However, the observations from the Chesapeake structure show that this phase may never actually be achieved until the crater is completely eroded and its entire geologic manifestation erased, such as, for example, by subduction.

**Perspectives for astrobiology**

The data provide insights into the influence of impacts on habitats for life during the early history of Earth, when impacts were more frequent than today (Abramov and Mojzsis, 2009). The Chesapeake structure yields evidence that the deep fracturing of rocks in the subsurface, or the emplacement of fractured rocks into the bottom of a crater cavity, can provide improved habitats for life underground. Although in the subsurface, nutrients are generally more of a limitation to life than pore space (Wellsbury et al., 1997), impact fracturing improves the flow of nutrients and redox couples for microbial life. During the early history of Earth, the planet was subjected to sterilizing impact pulses on its surface (Maher and Stevenson, 1988; Sleep et al., 1989; Abramov and Mojzsis, 2009). The data from the Chesapeake structure show that impacts would have created deep refugia (Sleep and Zahnle, 1998) in which life would have been protected from the destructive effects of subsequent impacts.

Impact fractured and vesicularised rocks could also have provided protection for photosynthetic organisms from the more intense UV radiation environment on the early Earth when the planet lacked a significant ozone shield (and speculatively on any anoxic planet with impact-shocked substrates on its surface). Samples of impact-shocked gneiss from Haughton impact structure containing the cyanobacterium, *Chroococcidiopsis*, were flown to the International Space Station and exposed for 22 months on the outside of the station to a simulated early
earth UV flux using the extraterrestrial spectrum and cut-off filters. It was empirically demonstrated that shocked rocks could have provided a refugium for life under the worst-case flux assumed for the early Earth (Bryce et al., 2014).

The study of the microbiology of impact craters also reveals insights into the potential influence of impacts on habitability elsewhere. Transient hydrothermal systems represent an obvious potential habitat for life in these contexts (Newsom, 1980; Osinski et al., 2001; Rathburn and Squyres, 2002; Koeberl and Reimold, 2004; Abramov and Kring, 2005; Squyres et al., 2008; Hode et al., 2009; Osinski et al., 2013), although they may be less abundant and in some cases more short-lived than volcanic hydrothermal systems (Pope et al., 2006). On Mars, impact craters may harbour deep subsurface locations where fractured rocks would enhance water flow in aquifers and geochemical turnover, possibly in combination with deep hydrothermal systems. In particular, future robotic and human exploration efforts on Mars might focus on the search for geological interfaces within craters where fluid flow between lithological units has enhanced the availability of energy and nutrients. These locations would be promising regions for deep drilling efforts to assess the geological conditions and potential habitability of that planet in its early history. In summary, the formation of hydrothermal systems, intra-crater lakes, fractured and permeabilised target rocks and geological interfaces all show the high potential of impact craters as sites to test the hypothesis of life on Mars and explore the formation of habitable conditions.

**Summary**

Asteroid and comet impacts exert lasting and important effects on microbial patterns of colonization in and around their craters. Future observations should improve our understanding of how physical and chemical changes in differing impact lithologies influence the abundance, diversity and distribution of microorganisms today and in the past and how geochemical changes in and around impact craters influence the availability of nutrients and redox couples for microbial communities. By coupling surface and subsurface microbiological studies of craters, the influence of impacts on global microbial processes will be better understood and the implications for life on the more violent early Earth can be examined. As impact events are a universal process, the study of their effects on a microbiota will yield insights into the potential for life in the face of impact bombardment elsewhere and where we might search for life and investigate the conditions for habitability in locations such as Mars. Paleobiological studies will advance our understanding of the early stages of the interactions of microbial life and impact cratering; for example, the study of ancient intra-crater hydrothermal systems, lake sediments, and impact metamorphosed rocks and their preserved biota will yield better insights into how to search for signatures of fossilized life on Earth and elsewhere.
References
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